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ECOLOGICAL CONTROL OF THE OCCURRENCE OF BARNACLES IN THE MIRAMICHI ESTUARY

BY

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ECOLOGICAL CONTROL OF THE OCCURRENCE OF BARNACLES IN THE MIRAMICHI ESTUARY

INTRODUCTION

Benthic marine organisms in estuaries encounter a wide range of ecological conditions. Within the estuary a variable influx of fresh water from the land is constantly being mixed with salt water from the sea through the action of regularly oscillating tidal currents. The adult animals on the bottom thus undergo constantly changing conditions of salinity, temperature, food supply, and other life necessities.

In spite of the bounteous supply of nutrient materials inherent in estuaries such as the Miramichi, the existence of bottom animals such as barnacles is precarious. Their planktonic larvæ are dispersed rapidly away from the spawning area by the tidal currents, both seaward and landward. River currents, winds, and other agencies superimpose on the tidal currents a net drift or residual flow, and the resultant movement of the water from all these influences is seaward. Hence we might expect the larvæ to be carried out of the estuary during their brief planktonic life span and relatively few to be left for attachment at their place of origin. During subsequent growth to maturity the young barnacles are further depleted by several kinds of bottom predators, and by myriad encrusting organisms that overgrow and smother the new colonies. How populations of barnacles may be maintained in estuaries despite the rigorous ecological conditions of the environment is therefore the chief problem of this study.

The presence of sedentary adult barnacles in an estuary presupposes that the range of ecological conditions in the area permits survival and that some of the attachment-stage larvæ are transported to the location from which they were initially dispersed. If the limits of distribution and numerical abundance of the adult population in the estuary are known, the range of temperature, salinity, and other conditions tolerated by the population may be measured directly. If the distribution and abundance of each of the larval stages are known, the influence of the water circulation on the dispersal of the larvæ may be deduced from changes in the location of successive life stages. The present investigation is thus concerned primarily with the ecology of the organism and secondarily with certain hydrographical features of the particular estuarine environment. On this basis of priority the ecological observations on barnacles have been given in "Observations" of the main text, and those on the hydrography of the Miramichi have been published separately (1955).

The three species of barnacles regularly occurring in the Miramichi area illustrate three types of estuarine distribution. *Balanus balanoides* L. and *B. crenatus* Brug. are arctic-boreal marine species of the outer coast that penetrate the outer estuary; (1) the former species occurs almost entirely above, and (2) the latter almost entirely below low water. (3) *Balanus improvisus* Dar. is a mediterranean-boreal brackish-water species that occurs mainly inside the estuary and is relatively scarce along the outer coast; like *B. crenatus* it occurs mostly below low tide. The larvæ of these species similarly show three types of distribution, dependent upon differences in the distribution of the spawning adults and in the effectiveness of dispersing agencies following spawning periods.

The life history of barnacles has been known for more than a century. The nauplius larva was discovered by Thompson (1830); the early development described by Groom (1894); and metamorphosis from cyprid to adult clarified by Doochin (1951). The eggs are fertilized internally and develop and hatch within the parental mantle cavity. The larvæ are liberated into the sea as non-feeding first-stage nauplii possessing three pairs of swimming appendages and a simple median eye. They metamorphose rapidly to the long-lasting plankto-trophic nauplius stage II. The normal larval sequence in barnacles consists of six nauplius stages and a cyprid stage, although considerable variability in the morphology of each stage (Norris, *et al.,* 1951) has led to reports of seven (Hudinaga and Kasahara, 1942) and eight (Herz, 1933) nauplius stages in species of *Balanus*. The bean-shaped non-feeding cyprid undergoes a change in swimming behaviour, descends to the bottom, and attaches by means of its paired antennæ to a suitable substratum. Metamorphosis of the cyprid to the young adult stage involves an ecdysis of carapace, compound eyes, and appendages, and a change in position of the internal organs. The period of growth to maturity of the sessile stage varies according to the species from three months to two years, depending chiefly on the water temperature.

Barnacles lend themselves favourably to ecological investigation. Both adult and larval stages are abundant in the area and may readily be collected in numbers sufficiently large for quantitative studies of distribution. The individual larval stages of barnacles are readily identified and enumerated even at low magnifications (16X). Because the adult population is permanently fixed, the starting point for the dispersal of the planktonic larvæ is known and their subsequent movements may be traced.

The Miramichi is a shallow coastal plain estuary into which discharges the entire surface run-off from the Miramichi drainage basin on its way to the sea (Figure 1). The watershed, located in central New Brunswick, Eastern Canada, is more than 125 miles in length and 5,450 square miles in surface area (Bousfield, 1955). The total length of the estuary proper, from the head of tide in the two main river branches to the chain of barrier islands across the mouth at the Gulf of St. Lawrence is nearly 50 miles. The mean low water depth for the entire estuary is 13 feet, and for the narrow channel, approximately 25 feet. Although the tidal zone has a vertical range of 5 to 6 feet, the mean tidal difference is only 2·4 feet owing to diurnal inequality of the tides in this region.

During each complete tidal cycle the average water exchange with the Gulf during the summer is approximately 15 per cent (Bousfield, 1955). A strong seaward drift at the surface and a landward counter drift along the bottom are superimposed on the wind and tidal currents by the influx of river water at the landward end of the estuary. The boundary between these oppositely drifting layers of water, termed the *level of no net motion,* occurs at a depth of approximately 10 feet. The seaward flow is strongest

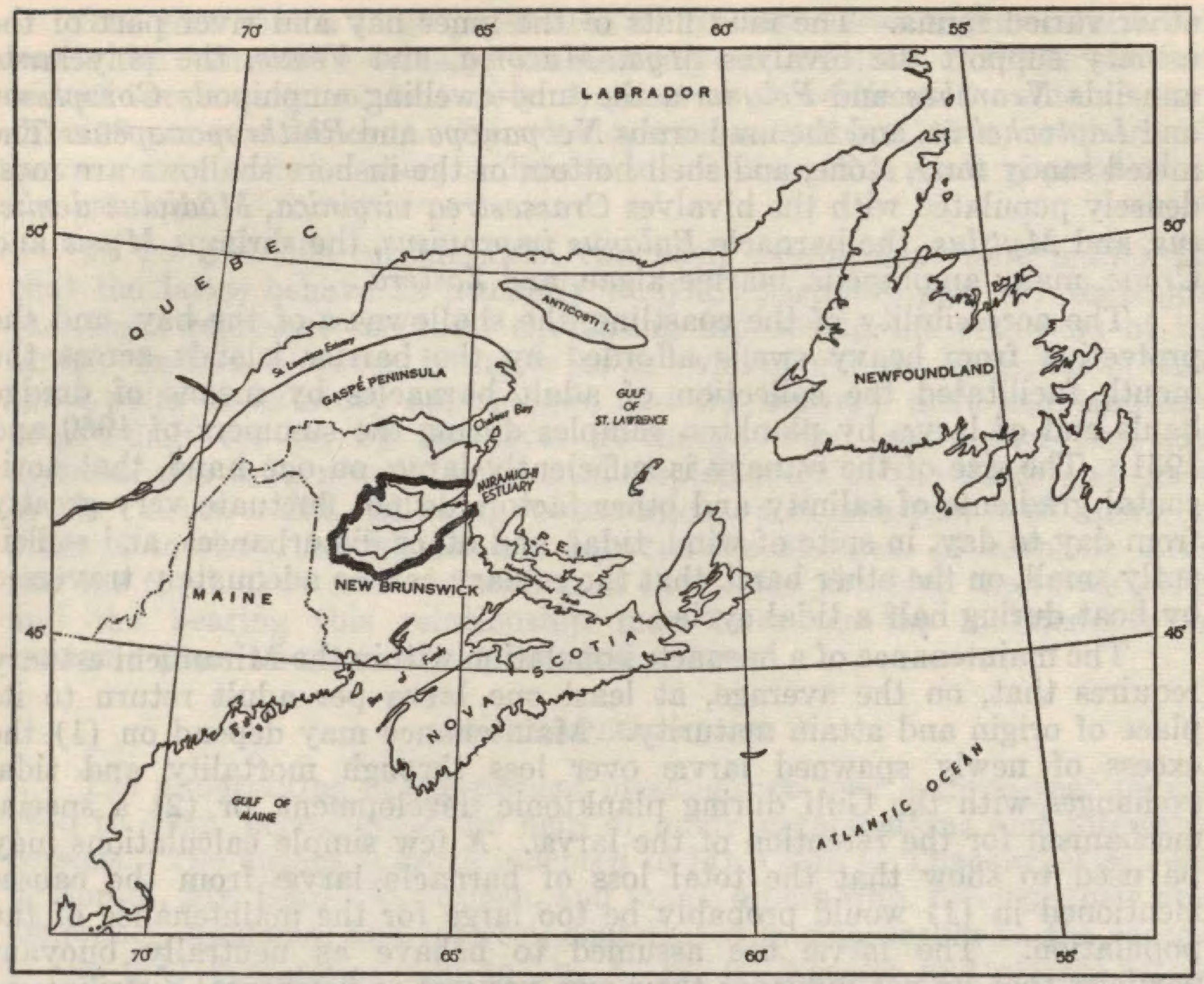

Figure 1. The Atlantic Coast of Canada showing location of the Miramichi drainage basin.

during the melting of snow and ice in the watershed in April and May (river discharge=25,000 cubic feet per second, but least during the dry season of August and September (discharge=4,000 c.f.s.). Heavy precipitation over the watershed is reflected immediately by strong freshets. Salinities range from 0 ‰ at the head to more than 25 ‰ at the mouth, and at any point are minimal during prolonged freshets (e.g. spring thaws) and maximal during the dry season. Surface water temperatures range from the freezing point during the five-month winter period to more than 20°C. during July and August, and the tidal zone is exposed to even greater extremes of temperature. Water temperatures in summer are slightly higher landwards and at the surface, than seawards and at the bottom. Water transparency is greater in the Gulf and on the north side of the estuary than near the head and on the south side.

The tidal zone supports a fauna of relatively few but conspicuous species that include the bivalves *Mytilus edulis* and *Mya arenaria,* the periwinkles *Littorina* spp., and *Nassa obsoleta,* certain small crustaceans such as *Gammarus* spp., *Orchestia,* and *Jaera,* and on sandstone outcrops, boulders, and pilings the barnacle *Balanus balanoides* and the attached algae *Fucus* and *Enteromorpha.* On the sandy bottoms of the Gulf and outer estuary may be found the bivalves *Spisula* and *Cyprina,* the echinoderms *Asterias, Strongylocentrotus,* and *Echinarachnius,* the large crustaceans *Homarus, Cancer,* and *Pagurus,* the barnacle *Balanus crenatus,* and other varied fauna. The mud flats of the inner bay and river part of the estuary support the bivalves *Mya, Macoma,* and *Venus,* the polychaete annelids *Neanthes* and *Polydora,* the tube-dwelling amphipods *Corophium* and *Leptocheirus,* and the mud crabs *Neopanope* and *Rhithropanopeus.* The mixed sandy mud, stone, and shell bottom of the inshore shallows are most densely populated with the bivalves *Crassostrea virginica, Modiolus demissus,* and *Mytilus,* the barnacle *Balanus improvisus,* the shrimps *Mysis* and *Crago,* many amphipods, marine algae, and *Zostera.*

The accessibility of the coastline, the shallowness of the bay, and the protection from heavy swells afforded by the barrier islands across the mouth facilitated the collection of adult barnacles by means of dredge hauls and of larvæ by plankton samples during the summers of 1950 and 1951. The size of the estuary is sufficiently large, on one hand, that horizontal gradients of salinity and other factors do not fluctuate very greatly from day to day, in spite of wind, tidal, and other disturbances, and sufficiently small, on the other hand, that the estuary can be adequately traversed by boat during half a tidal cycle.

The maintenance of a barnacle population within the Miramichi estuary requires that, on the average, at least one larva per adult return to its place of origin and attain maturity. Maintenance may depend on (1) the excess of newly spawned larvæ over loss through mortality and tidal exchanges with the Gulf during planktonic development, or (2) a special mechanism for the retention of the larvæ. A few simple calculations may be used to show that the total loss of barnacle larvæ from the causes mentioned in (1) would probably be too large for the maintenance of the population. The larvæ are assumed to behave as neutrally buoyant particles that do not influence their own vertical or horizontal distribution.

As a result of circulation alone, the population of larvæ 'P_m' remaining after being depleted from its initial size 'P_o' by a series of tidal cycles and not receiving recruitments from upstream or downstream during the interval is given by

$$P_m = P_o(1\text{-}r)^m$$

in which 'm' is the number of tidal cycles, and 'r' is the exchange ratio, defined as the proportion of water moving seaward during each tidal cycle which does not return on the following flood tide (Ketchum, 1952). The duration of planktonic existence in *B. improvisus* in the Miramichi estuary is approximately 18 days or 36 tidal cycles (page 44). As noted already on page 2 the exchange ratio for this estuary is approximately 0·15. A maximum fecundity of 10,000 larvæ per adult (page 8) may be assumed. Substituting these values in the equation above:

$$\begin{aligned} P_{36} &= 10^4\ (1\cdot0\text{-}0\cdot15)^{36} \\ &= 10^4\ (0\cdot85)^{36} \\ &= 29 \end{aligned}$$

Thus, less than 1 per cent of the larvæ would remain inside the estuary at the end of the eighteen-day period. Assuming 10 per cent survival during this period also, barely three larvæ would reach the original site, on the average. If natural mortality during attachment and growth of spat to maturity (probably more than 90 per cent) is also taken into account, less than one larva per adult would reach maturity. The barnacle population in the Miramichi could probably not be maintained under these conditions and under the assumptions made.

The fact that a large population of *B. improvisus* is maintained well inside the Miramichi estuary, year after year, indicates that the seaward loss of larvæ may not be nearly so great as the estimated value of more than 99 per cent (above). By what special mechanism, then, are barnacle larvæ retained in numbers sufficient to maintain the adult population in the estuary?

In the previous consideration two basic assumptions were made: (1) that the larvæ behave as neutrally buoyant particles, and (2) that tidal exchanges represent the total circulation influencing the transport of the larvæ. In fact, however, barnacle larvæ swim effectively by means of their three pairs of natatory appendages, and the seaward drift and landward counterdrift set up by the river discharge, wind, and other non-tidal agencies also influence the horizontal displacement of the water and hence of the larvæ. The following observations and analyses will therefore attempt to show the relationship between the dispersal of barnacle larvæ and the residual or drift circulation at the depths at which the larvæ swim, and the bearing this relationship may have on the maintenance of barnacle populations in the Miramichi estuary.

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REVIEW OF THE LITERATURE

The distribution of sessile marine organisms in estuaries has been explained by many authors in terms of the survival of the adult stage under the existing environmental conditions. For instance, peculiarities in the distribution of adult barnacles in Puget Sound have been attributed to wave and current action, salinity, temperature, exposure, desiccation, and other survival factors (Rice, 1931). A limited spatial relocation of some adult barnacles may be caused by the action of currents, ice, and man, on stones, shells, eel grass, ships, lobster pots, and other suitable substrata to which the animals are attached (Millard, 1950). More recently Rogers (1940), Huntsman (1945), and Carriker (1951) have stressed the importance of the retention of planktonic larval stages in maintaining adult populations within the estuary. Retention of the larvæ is a function of the initial abundance, rate of mortality, and duration of planktonic existence of the larvæ and of the water circulation at the depths at which the larvæ swim.

Distribution and Survival of Adult Barnacles

Much of the previous work on the ecology of adult barnacles has concerned their tolerance to low salinities. Precise data from physiological experiments on Miramichi species of barnacles are lacking. However, the limits of distribution of these and other ecologically similar species in other estuaries have been correlated with corresponding values of salinity. Pilsbry (1916) noted *B. improvisus* in very low salinities in the Quinnipiac River, Massachusetts, and recorded *B. eburneus* associated with fresh-water snails on pilings far up Chesapeake Bay. Of at least nine species of barnacles in the Knysna estuary, South Africa, two species (*B. amphitrite denticulata* and *B. elizabethae*) were found almost to the head of tide, 9 miles above the mouth, whereas the other seven species penetrated in from the sea much shorter distances (Day, *et al.*, 1952). Millard (1950) correlated the upriver limits of distribution of seven of the nine species in the Knysna with the distribution of July (rainy season) minimum salinities.

The lower lethal limit of salinity in barnacles and other marine macro-crustaceans probably depends upon the previous acclimation to low salinities, to the length of exposure, and to the water temperature, as McLeese (1950) has illustrated experimentally in the American lobster. Low salinities may retard, even prohibit, reproduction in many euryhaline marine animals that live in the most landward part of estuaries (Ekman, 1953). Butler (1949) found a delay of seven weeks beyond normal in the maturation and spawning of *Crassostrea virginica* under conditions of abnormally low salinities (less than 10 ‰).

Marine animals may be grouped according to their requirements of salinity. Dahl (1948) has revised previous classifications of the coastal marine environment based on the saltiness of the water, and has advanced as most widely applicable the system of Redeke-Valikangas (1933):

			Range of Salinity (‰)
Fresh water			< 0·5
Brackish water	**Oligohaline**		0·5 – 3
	Mesohaline	**Meiomesohaline**	3 – 8
		Pleiomesohaline	8 – 16·5
	Polyhaline		16·5 – 30
Marine water			> 30

Specific fresh-water organisms tolerate only trace amounts of salt and are found only at the heads of estuaries. Specific marine forms tolerate little dilution of sea water and are restricted to the open coasts. Shallow water coastal animals find their home in the polyhaline-brackish zone, which, in estuaries, is usually located near the mouth. Brackish-water forms are centred in mesohaline waters, and well inside the estuary. The application of this system to the Miramichi estuary, and the grouping of barnacles and other benthic organisms in these categories of salinity are discussed on page 53.

The influence of water temperature is probably greater on the vertical than on the horizontal distribution of barnacles in estuaries. The difference in temperature between head and mouth of shallow coastal plain type estuaries at any time is relatively small, whereas that between surface and bottom may be large owing to vertical stratification of the water. In winter, when water temperatures are close to the freezing point, even slight vertical differences become significant. Blegvad (1929) and Smidt (1944) observed severe mortality in animals of the upper littoral (tidal) zone following severe ice winters. Death of the animals (e.g. *Mytilus edulis*, *Littorina littorea*) was attributed to freezing of the tissues or lack of oxygen, or both. In summer, excessive heating of the inshore shallows and exposed tidal zone might become lethal to certain cold-water species.

The seasonal range of water temperature may have an indirect influence on the horizontal distribution. For instance, the three species of barnacles in the Miramichi estuary spawn at different temperatures and therefore at different seasons (Bousfield, 1954), and the degree of dispersal of the larvæ varies according to the river discharge at the time.

The nature of the substratum plays an important part in the local distribution of barnacles. The distribution of *Balanus balanoides* and *Chthamalus stellatus* may be related to the lithology of the coastline (Moore, 1936; Moore and Kitching, 1939). In general, survival is greater on hard rocks (e.g. chert) than on soft rocks (e.g. chalk) that are exposed to abrasion by waves and ice.

The influence of predation on the local distribution of barnacles depends upon the degree of overlapping of ecological requirements of both prey and predator. Adult barnacles of the Miramichi region are preyed upon by starfish (Bousfield and Logie, 1947) and probably also by *Thais* and other whelks (Moore and Kitching, 1939), nemerteans, polychaetes (e.g. *Eulalia*), turbellarians (e.g. *Eustylochus*), other slowly moving bottom invertebrates, and certain fishes. As such animals are scarce in brackish water, their depredations on barnacle populations would be great only near the mouths of estuaries.

Where water temperature, salinity, food supply, and other ecological conditions are optimal for survival, the local distribution of barnacles may be limited by competition for space with other types of encrusting organisms. Growing barnacles may be smothered by bivalves such as *Mytilus*, *Congeria* (van Breeman, 1933), or by bryozoans, sponges, hydroids, and tunicates (Weiss, 1948). The maximum abundance of each barnacle population is limited also by intraspecific competition. Owing to gregariousness, or the tendency for individuals to crowd together during attachment (Knight-Jones, 1950), the density of the population of barnacles on suitable substrata frequently reaches a saturation point. Thus, growing barnacles crowd out weaker ones, and some are in turn smothered by more spat growing on top of them.

The data on the rate of mortality of adult barnacles determined by all such factors combined have been reviewed by Moore and Kitching (1939). The annual rates of mortality in fully adult *B. balanoides* and *Chthamalus stellatus* range from 3 per cent to 96 per cent at highest high-water and lowest low-water levels of the tidal zone, respectively. The annual rates of mortality of the species at the low-water line on the coast of Plymouth are 36 per cent and 46·5 per cent respectively. Thus mortality in species living below the tide lines may be still greater.

Dispersal and Survival of Barnacle Larvæ

With respect to the retention of the planktonic larval stages of barnacles in estuaries, certain prerequisites may first be considered. Newly spawned larvæ are released in the vicinity of the adults on the bottom. From this point of origin the larvæ tend to be dispersed up and down the estuary by the circulation, but the net drift of the water mass as a whole must be seawards because of the river discharge. Despite the seaward loss and natural mortality of barnacle larvæ, a certain number are carried back to the original spawning site by the time of attachment in ways that will be examined.

The size of the initial population of larvæ will depend upon the density of the adult population, the fecundity of the species, the prolongation of the spawning season, and other factors. The fecundity of individuals of *Balanus balanoides* is greater where the adult animals are crowded together (Kuznetzov and Matveeva, 1949). The production of organic soft parts (including reproductive tissue) in relation to total body weight is greater, and the success of cross-fertilization is more complete under such circumstances. Fecundity is also proportional to the size and age of the individual. Thus the average number of ripe eggs (or larvæ) produced per individual per year in Murmansk populations of *B. balanoides* ranged from 540 in the first year of spawning (density of adults about 12 per sq. in.) to 7,393 in the third year (density about 30 per sq. in.). Comparable figures for *B. crenatus* and *B. improvisus* are not available. The fecundity of both species would probably be greater than that of *B. balanoides,* however; in *B. crenatus* individuals of a given age are larger, and in *B. improvisus* (similar in body size to *B. balanoides*) the eggs are much smaller and thus more numerous per unit of ovigerous tissue. The fecundity of adult *B. improvisus* might be estimated between 1,000 and 10,000 nauplii per individual per spawning period.

Factors Tending to Reduce Larval Abundance

The amount of seaward dispersal of zooplankton depends upon the magnitude and direction of the estuarine circulation during the spawning season and upon the duration of planktonic development. Thorson (1950) concluded from many years of observation that a tremendous wastage of eggs and larvæ of shore-living species results from offshore movement of water in which the animals are swimming. The planktonic duration of the larvæ of the sand crab *Emerita* is four to five months, during which some larvæ may be carried more than one hundred miles from the coast (Johnson, 1939).

The larvæ of the brackish water *Balanus improvisus* are numerous in estuarine waters, but scarce outside. Because of tidal exchanges between estuarine and outside waters, river discharge, and other agencies of water circulation, the net transport of estuarine larvæ is seaward. In estuaries such as Barnstable Harbour, Cape Cod, where tidal exchange with the open ocean is great (90 per cent), the seaward loss of larvæ per tidal cycle is similarly large (Ketchum, 1952). In estuaries where this exchange is low

(12 per cent in Moriches Bay), relatively few larvæ are lost. In the nearly land-locked Oosterschelde, only 4 per cent of the larvæ of *Ostrea edulis* is lost seaward per tidal cycle (Korringa, 1952).

When the influx of river water to the estuary is large, a correspondingly large seaward loss of larvæ might be expected. Thus, larvæ spawned in the spring when rivers are at peak flood would be subjected to greatest flushing of the estuary and greatest seaward loss; those spawned in late summer to least flushing and least seaward loss.

The spawning season of Miramichi species of barnacles takes place during the period March to October (Bousfield, 1954). The larvæ of *Balanus balanoides* occur in greatest abundance from April 1 to June 1; those of *B. crenatus* from mid-April to July and again in October; and those of *B. improvisus* from June 1 to mid-August and again in September and October. Peak attachment of cyprids takes place in *B. balanoides* during early May; in *B. crenatus* from mid-May to mid-June; and in *B. improvisus* from mid-June to the end of July. The relation of seaward dispersal of barnacle larvæ to the magnitude of discharge of the Miramichi River at these times is discussed in a later section (page 59).

The duration of planktonic existence varies considerably, according to the species, and depends primarily on water temperatures. The duration of the larval stages of certain barnacles on the Atlantic Coast of America is given in Table I. In general, the duration is shorter at higher temperatures. Estimates of the duration of larval life in *B. improvisus* range from

TABLE I

Duration of larval stages of barnacles occurring on the Atlantic Coast of America

Species	Authority	Temp. ° C.	Duration of larval stage							
			Nauplius (days)						Cyprid (days)	Total
			I	II	III	IV	V	VI		
B. balanoides	Pyefinch (1948) Clyde River	4–5°	<1	6	3	6	3	15	3–14	5 weeks
B. balanoides	Pyefinch (1948) Clyde River	5–6°	<1	3	3	6	6	6	?	3–4 weeks
B. balanoides	Bousfield (1954) Halifax Hbr.	3°	<1	7	4	6	5	6	?	5+ weeks
B. crenatus	Pyefinch (1948) Clyde River	4–5°	few hrs.	11	3	6	3	6	?	30 days
B. crenatus	Pyefinch (1948) Laboratory	15°	<1	7	3	2	2	1	<3	16+ days
B. eburneus	Grave (1933) Woods Hole	15°–20°	?	?	?	?	?	?	?	7–10 days
B. improvisus	Graham *et al.* (1945) Oakland, Calif.	>16	?	?	?	?	?	?	?	2 or more weeks (approx.)

approximately two weeks at Oakland, California, water temperature above 16°C. (Graham, *et al.*, 1945), to almost a month in the Zuider Zee, average temperature 16·9° C. (van Breemen, 1933), and more than a month in the Oslo fiord where surface temperatures during the summer are not much above 10° C. (Broch, 1924). The present estimates for this species in the Miramichi are shown on page 44.

The reduction in numbers of barnacle larvæ through natural mortality is considerable. Predation and food supply are probably the principal biological factors, and extremes of temperature and salinity are the physical factors that contribute to high rates of larval mortality. Larval barnacles are assumed to be preyed upon by most animals that feed on plankton, including the young and adults of certain fishes, larval decapod crustaceans, shrimps, comb jellies, arrow worms, and some copepods (e.g. *Temora, Centropages*); and by bottom organisms such as the mud blister worm (*Polydora*), barnacles (*Balanus*), and bivalves (*Crassostrea, Mytilus*). Barnacle nauplii feed on small diatoms, protozoa, green algæ, small green flagellates, and organic particles (Lockhead, 1936). Mortality may result on one hand from lack of such food, and on the other hand from the superabundance of certain kinds of nannoplankton (Loosanoff and Engle, 1947; Korringa, 1952) and diatoms (Hardy, 1936) which may produce metabolites toxic to zooplankton. Pyefinch (1948b) attributed the abnormal disappearance of larvæ of *B. balanoides* in April to a large outburst of the diatom *Skeletonema* during the same period. Barnes (1950), however, found no unusual depletion of larval stocks during diatom outbursts.

Water temperatures in estuaries probably do not reach lethal limits for barnacle larvæ, except near the beginning and end of the spawning season. The range of water temperatures in which the larvæ are known to survive (Bousfield, 1954) are as follows:

B. balanoides—freezing point to 15°C.
B. crenatus—freezing point to 18°C.
B. improvisus—10° to 30°C.

Data on values of salinity lethal to barnacle larvæ are not available. According to the species, these levels would depend upon the previous acclimation to low salinities. These lower limits have been estimated for Miramichi species in the section under "Observations".

Factors Tending to Retain Larvæ in Estuaries

Vertical Movements

In relation to the amount of transport of larvæ in a horizontal plane by water movements, that by swimming is practically negligible, whereas in a vertical plane, that by swimming may be very great. Vertical movements enable larvæ to escape from seaward-moving water layers and thus remain within the estuary. Data on the rates of swimming of barnacle larvæ are not available. Korringa (1952), however, gives a value of 0·4 cm./sec. for the rate of sinking of a quiescent oyster larva with velum expanded. Minimum swimming rates necessary to overcome sinking in barnacle larvæ of similar size may be of this order of magnitude. Assuming that this swimming velocity (0·4 cm./sec.) could be maintained also in a given horizontal direction, allowing no time for vertical migration, moulting, and other life processes, the total horizontal displacement due to swimming would be only 6 miles during the entire life cycle (18 days). At an average current velocity of only one knot (50 cm./sec.) a corresponding displacement by tidal currents would be effected in about half a tidal cycle (6 hours). On the other hand, a larva swimming vertically at a rate of 0·4 cm./sec. could traverse the mean depth range of the Miramichi estuary (5 meters) in 20 minutes. In the James estuary vertical velocities of water currents at maximum horizontal flow (1 to 2 knots) are of the order of only 0·01 cm./sec. (Pritchard, 1952), a value much less than that of the assumed possible swimming rate of the larvæ.

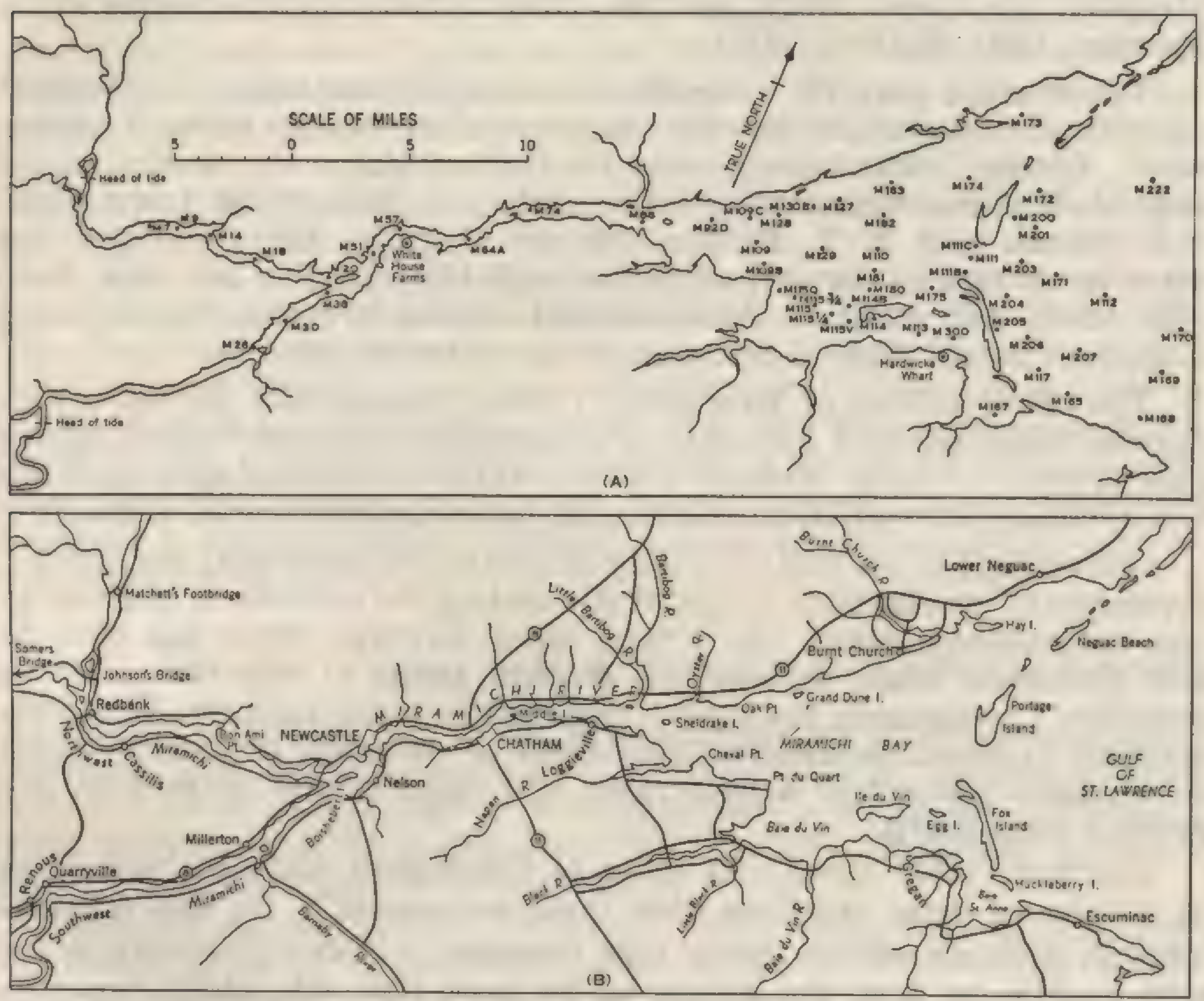

Figure 2. Topographical features of the Miramichi estuary.
(A) Principal hydrographic stations, 1951.
(B) Place names, rivers, and roads.
(Courtesy R. A. McKenzie, Chatham, N.B.)

The vertical distribution of barnacle larvæ appears to be controlled mainly by sinking and swimming in response to changing conditions of light intensity, salinity, temperature, and other factors. Evidence provided by Broch (1924), Fales (1928), Ishida (1936), Bassindale (1936), and Treat (1937) indicates that both the intensity and direction of light stimulate oriented swimming movements in nauplii of *B. balanoides*, *B. improvisus*, and many other barnacle species. Visscher and Luce (1928) suggest that cyprid-stage larvæ of *B. improvisus* may undergo vertical migrations in response to a change in light intensity from daylight to darkness. The cyprids of *B. improvisus* and other barnacle species are stimulated to attach by diffuse light of low optimum intensity (Weiss, 1947; Smith, 1948). The results of Visscher (1928), McDougall (1943), Pyefinch (1948a), and Barnes, *et al.* (1951) indicate that the cyprids of barnacles living in the tidal zone (i.e. *B. balanoides, Chthamalus stellatus, B. eburneus*) orient towards the light source at the time of attachment, whereas those living at greater depths (i.e. *B. improvisus, B. crenatus, B. amphitrite*) orient away from it.

Other planktonic organisms that respond directionally to light stimuli include the larvæ of the American oyster (Carriker, 1951), the European flat oyster (Korringa, 1952), and the small neritic copepod *Acartia tonsa* (Esterley, 1920; Shallek, 1943).

Temperature may be a significant factor in controlling the vertical movements of zooplankton in estuaries where a thermocline exists (Cushing, 1951). Clarke (1933) found that in the Gulf of Maine the evening movement of *Metridia lucens* toward the surface halted at the thermocline. T. C. Nelson and E. B. Perkins (as per Carriker, 1951) thought that oyster larvæ rose to the surface during high temperatures but sank down again during cold weather. In subsequent studies, however, Perkins found no appreciable influence of temperature on oyster movements.

The investigations of Bainbridge (1949) indicate that phytoplankton gradients stimulate both horizontal and vertical movements of zooplankton in the presence of light. Nothing is known of the influence of such gradients in determining the vertical distribution of barnacle larvæ in the Miramichi.

One concept of the role of salinity in controlling horizontal and vertical movements of zooplankton is that of stimulating the animals to swim away from unfavourable zones. In several cases, however, there has been no clear distinction made between the limiting action of this factor on the survival of the organism and that of dispersal by water currents. Gradients necessary to stimulate directed movements of estuarine organisms, which are normally tolerant of a wide range and rapid change in salinity, are probably quite sharp.

Carriker (1951) noted that larvæ of *Crassostrea virginica* "remain in the vicinity of sharp haliclines when these are present". He also substantiated T. Nelson's earlier theory that changing salinities stimulate oyster larvæ to swim up from the bottom on the flood tide. He added, however, that much further investigation is necessary to determine the minimum increment of salinity which, when added to the effect of tidal velocity, would provide such a stimulus.

Barlow (1953) observed that the nauplii of *Acartia tonsa* were abundant in a wide range of salinities (8‰ to 25‰) and usually equally numerous from top to bottom even when the vertical gradient was more than 10 ‰ in 6 feet. Within this range of salinity he found at times, however, marked differences in abundance of nauplii between surface and bottom, although the corresponding differences in salinity were only 2 ‰ to 5 ‰. Perhaps a gradient of salinity necessary to stimulate movement need only be small near the lethal level.

Rogers (1940) attributed the concentration of barnacle larvæ (*B. improvisus*?) in bottom layers near the head of the St. John estuary to a tendency to avoid the fresh water of surface layers.

Horizontal Transport

The relative importance of tidal currents and non-tidal drifts in the horizontal transport of zooplankton is a feature peculiar to each estuary. In tidal estuaries with little or no land drainage, the water circulation is determined mainly by the ebb and flow of tidal currents. Within a given estuary, the maximum current velocity and amount of water turbulence are proportional to the amount of tidal rise and fall. In tidal estuaries where land drainage is considerable, the strength of the ebb current is considerably augmented by the seaward flow of fresh water, whereas that of the flood current is correspondingly reduced. The difference in velocity between ebb and flood currents represents the residual or net drift. Because the light fresh river water tends to float over the heavier salt water, during a complete tidal cycle the movement tends to be seawards near the surface, landwards near the bottom (Bousfield, 1955). At some intermediate depth there is no residual movement either seaward or landward, and this depth is termed "the level of no net motion" (Pritchard, 1951, 1952). Thus larvæ near the surface in such estuaries may be transported in a much different direction and at a different velocity than those near the bottom or at some intermediate depth. On this consideration it will be shown (p. 46) that the amount of seaward dispersal of barnacle larvæ in the Miramichi estuary is much less than would be the case if the animals displayed a uniform vertical distribution and if tidal exchanges were the only transporting agency.

Previous Theories of Zooplankton Retention in Particular Estuaries

Previous considerations of the vertical swimming movements of various estuarine zooplankton in response to gradients of light, salinity, temperature, and other factors, and of the differential velocity and direction of water currents with depth and stage of tide, have contributed to several theories of larval retention in estuaries.

In the Miramichi estuary Huntsman (1945) found both benthic adults and pelagic larvæ of the barnacle *B. improvisus* and the mud crab *Rhithropanopeus harrisii* well up the estuary but not in the outer water. As zooplankton near the surface would be carried seawards in the residual surface outflow of fresh water, he predicted that the larvæ of these species must be near the bottom most of the time. Rogers (1940) observed a concentration of barnacle larvæ (*B. improvisus*), arrow worms (*Sagitta elegans*), and smelt larvæ (*Osmerus mordax*) far up-river in the Miramichi and St. John estuaries. He attributed the landward transport of these animals to the landward drift of salt water along the bottom. He postulated, but did not test experimentally, the theory that vertical migration of the smelt larvæ in response to daylight and darkness would carry the negatively phototactic larvæ into the bottom layer for a greater length of time than into the seaward flowing surface layer, and thus the population would move landward.

A different explanation makes use of a difference in vertical distribution of larvæ between ebb and flood tides. Carriker (1951) noted in Delaware Bay that the seaward flow on the ebb (presumably at the surface) was of longer duration than the landward flow on the flood. He estimated that the resultant seaward flow during the 14-day (27 tidal cycle) planktonic existence of oyster larvæ in this estuary would have resulted in a seaward movement of larvæ of some 20 miles if they remained at the surface. None the less, some larvæ attached as much as 20 miles *above* the spawning beds.

Carriker's theory for the retention of oyster larvæ in New Jersey estuaries was based on a knowledge of the horizontal transport by water currents (wind, tidal, and other causes) and of the vertical distribution of the various larval stages at various stages of the tidal cycle. He confirmed the laboratory and field observations of T. C. Nelson and E. B. Perkins (1930), Roughley (1933), and Prytherch (1928) that oyster larvæ were generally more numerous in the plankton on the flood than on the ebb; that the younger stages drifted passively with the tide and showed no marked difference in vertical distribution with stage of tide; and that older stages dropped on or near the bottom during ebb tide and rose on the flood. He demonstrated clearly for the first time that relatively large numbers of mature and eyed larvæ may be present on the bottom during ebb tide. Thus, by sinking on the ebb and swimming up off the bottom on the flood the older stages tend to be transported landward to the headwaters of the estuary. His support of previous views that the stimulus to rise on the flood is provided by changing salinities has not been universally accepted, however.

Barlow (1953) studied the maintenance of an endemic population of copepods (*Acartia tonsa*) in a small tidal estuary of Cape Cod. He found a continuous loss of larvæ from the estuary attributable to natural mortality (predation, abrasion by silt in suspension, etc.) and seaward transport. He concluded that the 'replacement rate' of nauplii through reproduction and recruitment from those sinking into the inflowing bottom water was sufficient to account for the observed stability in the distribution and abundance of the population over a three-week period.

In a hydrographically closed coastal marine area of large size (the Gulf of Maine), Redfield (1941) has shown how an endemic population of calanoid copepods may be maintained by the pattern of horizontal non-tidal flow. The bulk of the copepod population is transported by the counter-clockwise current in a complete circuit of the Gulf basin every ten to twelve months. During this period the completion of the life cycle from egg to adult copepod makes possible the replenishment of the population depleted through mortality and seaward transport.

The results of other important studies of the dispersal of zooplankton indicate, on the other hand, that in certain estuaries no special mechanism for the retention of larvæ is necessary to account for the observed density of set. In Long Island Sound, Loosanoff (1949) found no general relation between the vertical distribution of oyster larvæ and the tidal cycle, and no evidence that larvæ in advanced stages were more common near the bottom, nor that they descended to the bottom on the ebb and rose again on the flood. Korringa (1952) commented that the larvæ of *Ostrea edulis* had been observed to make vertical migrations, alternately swimming and sinking in response to changes in light intensity, in the laboratory, but not in the Oosterschelde where tidal currents were strong, vertical mixing of the water thorough, and vertical stratification negligible. The vertical distribution of all age groups appeared to be the same at all hours of the day and night, in all types of weather, and during all stages of the tidal cycle. It is probable that in estuaries of low exchange ratios such as the Oosterschelde, where the loss of oyster larvæ is only 4 per cent per tidal cycle, the number of larvæ remaining in spite of seaward loss and mortality would be sufficient to ensure an adequate spatfall at upriver localities.

The following considerations are therefore important in deducing the mechanisms by which planktonic organisms are retained within tidal estuaries:

(1) The vertical distribution of the various life stages determined by swimming and sinking.
(2) Changes in vertical distribution resulting from tidal currents, turbulence, and other physical factors.
(3) The tidal exchange ratio of the estuary.
(4) The residual or non-tidal component of water movement at various depths.
(5) The total production and rate of loss of the population through mortality and seaward transport.

METHODS

The present investigation entailed collections and field observations of both adult and larval stages of barnacles and of organisms having similar ecological requirements. The occurrence of adult barnacles and other benthic animals in the Miramichi estuary was determined from bottom samplings. The distribution and abundance of barnacle larvæ were measured by means of weekly quantitative plankton samples throughout the area. Methods of obtaining hydrographical data at the plankton stations and at additional "check" stations (Figure 2), and of measuring river discharge, are given elsewhere (i.e. Bousfield, 1955).

Bottom Sampling

The distribution of adult barnacles was determined in August, 1950, and throughout the summer of 1951, by means of shore collecting and bottom dredging, and by sampling from buoys, stakes, and special test boards set out for the barnacle spat. An experimental model scallop drag was used successfully for the dredging of barnacles attached to large stones and shells on rocky, pebbly, or shelly bottoms. Owing to unpredictable fluctuations in the efficiency of the dredge over various types of bottom, the results are at best semi-quantitative. In trials over very shallow bottoms where the dredge could be observed, the efficiency of the drag in picking up and retaining all suitably sized objects varied between 25 per cent and 80 per cent (usually about 50 per cent). The total number of barnacles taken per standard haul (sampling 600 sq. ft. of sea bottom) was estimated from total counts of barnacles on each of five or six shells and stones in the sample. Numerical values for categories of abundance of barnacles are given in Table II (See also Figure 4).

On bottoms of pure mud or pure sand the Ekman quantitative sampler ("bite" 6 inches square) was employed effectively along with the drag. The bottom samples were washed down on a wire screen and the organisms picked out and preserved.

TABLE II

The numbers of barnacles per standard haul (600 sq. ft. of bottom) for categories of abundance used in Figure 4.

Species	Category of abundance			
	few	mod. numerous	numerous	very numerous
B. improvisus	100	100 – 1,000	1,000 – 10,000	> 10,000
B. crenatus	10	10 – 100	100 – 1,000	> 1,000
B. balanoides	<10*	>10*		

*Number per large boulder on the shore.

The rate and intensity of barnacle attachment in the river portion of the estuary were determined experimentally by placing special test boards and 'barnacle poles' (Figure 3) at localities mainly upriver from Newcastle (Table III, page 21). The wooden test panels, each 4 inches square, were strung on cod line at depths below low water of 1, 3, and 5 feet. The poles and test panels were first placed in position during the last week of June and visited at bi-weekly intervals in July and August. At low water the test panels could be hauled to the surface and lowered again by means of the cod line, and barnacles and other attached organisms identified and counted. At the end of August the poles and panels were taken up, and the poles were also examined for intensity of fouling. The number of barnacles per strip one inch wide around the circumference of the pole, at various levels in reference to the low water mark, were counted.

Plankton Sampling

The method of plankton sampling in 1951 was designed primarily to furnish a reliable picture of the average horizontal and vertical distribution of barnacle larvæ in the estuary and to show the amount of deviation from the average pattern throughout the summer. A series of plankton stations was set up in the Miramichi River with base of operations at the White House Farm and also in Miramichi Bay with headquarters near Hardwicke (Figure 2). This coverage allowed twelve to fifteen stations to be run by small power boat in a single cruise of six to eight hours (half a tidal cycle). The position of the plankton stations was established each time by lining up markers on the shore. This procedure was not possible after dark, and night-time observations were thus prevented. The pattern of plankton distribution is distorted somewhat from the true picture by the tidal ebb and flow during such a cruise. In order to minimize such

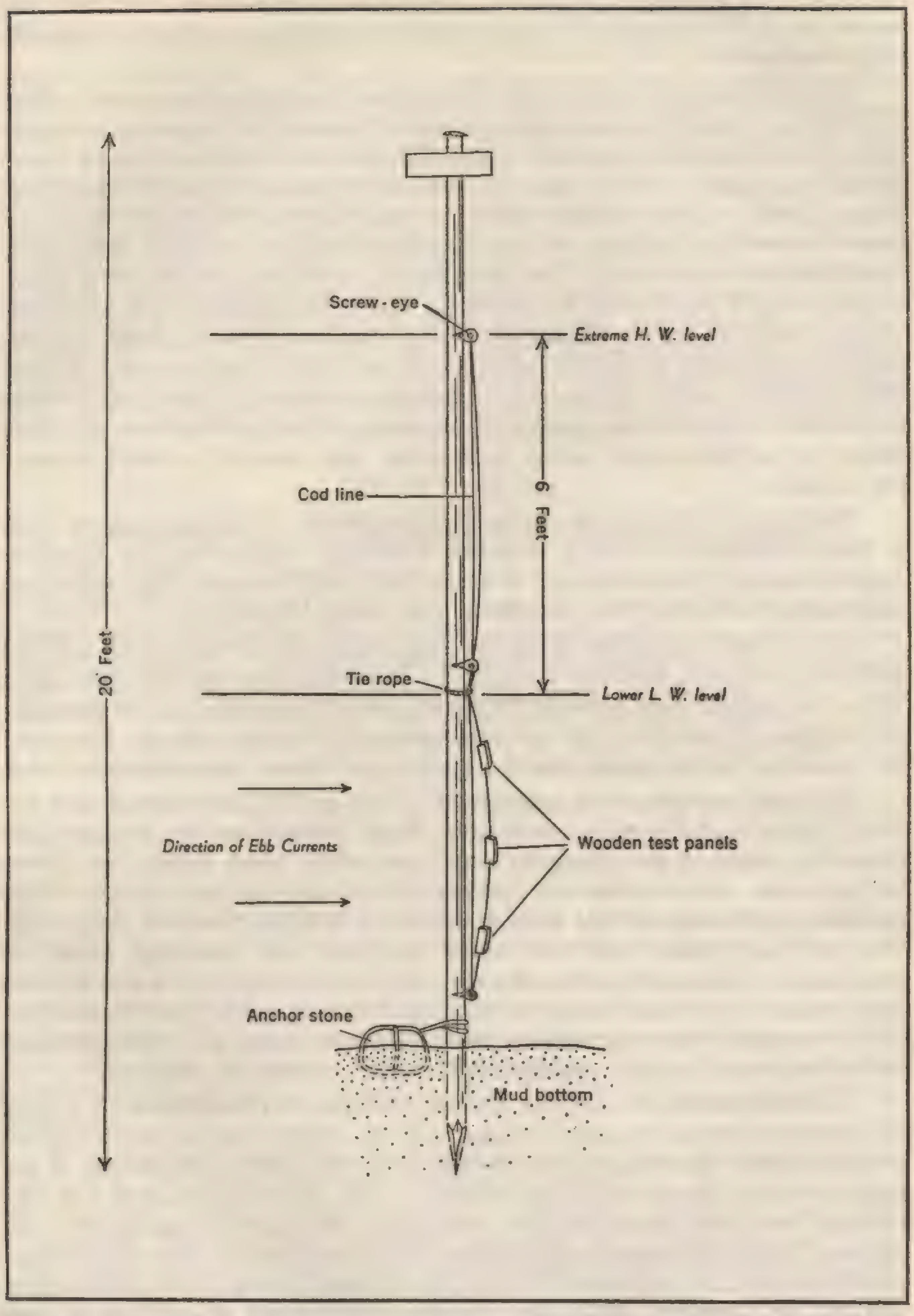

Figure 3. Barnacle pole apparatus used in the experiment to determine rate of settlement.

distortion, an attempt was made to commence the runs at half tide and return on the following half tide, rather than leave and return at opposite slack waters.

Plankton samples were taken by means of a portable pump and bolting silk of No. 12 mesh (size of aperture = 0·119 mm.). The pump consisted of a Johnson gasoline-powered motor fitted with a governor and a small centrifugal pump, all mounted on the same wooden base (Gibbons and Fraser, 1937). The one-inch rubber intake hose was calibrated in 3-foot intervals for measurement of depth, and terminated by a cast-iron nozzle fitted with a check valve. The governor of the motor was set for a pump delivery of 125 litres every 2½ minutes. The delivery was tested, according to the method of Barnes (1949), by filling a tank of known volume, and the delivery was found to vary by about ± 4 per cent. A volume of 125 litres was found to contain statistically adequate numbers of larvæ of *Balanus improvisus,* the principal species of barnacle studied. Moreover, the time taken for a three-depth series of samples was thereby reduced to only ten minutes.

Because of difficulty in controlling the depth of the pump hose from a boat anchored in strong currents, similarly experienced by Carriker (1951), the dory was allowed to drift freely and the sampling operation was begun just above and completed just below the station.

In making a plankton haul the hose water was first run off and the sample water then strained through a Clarke-Bumpus sampler net, fitted with a bucket and held beneath the outlet hose of the pump. After precisely 2½ minutes of sampling, the net was removed from beneath the hose, and the contents washed down into the bucket and poured into a labelled vial.

Plankton samples were preserved in 4 per cent (later reduced to 1 per cent) formalin at the end of each run. Slight but not serious alterations in the composition of the plankton may have taken place during the three- or four-hour interval between taking and preserving the sample. The possible significance of this error is discussed in a later section (page 42). The net was rinsed with sea water between each sampling operation and washed thoroughly with soap and lukewarm water at the end of each day's run. In spite of these precautions, however, a slight contamination of the samples was evidenced at times by the presence of dried specimens in the material, but the contamination could usually be detected.

The comparison of samples between stations was facilitated by taking all measurements at standard depths of 0, 12, and 24 feet, or to the nearest 6-foot interval depending on the proximity of the bottom, regardless of the stage of tide. The average rise and fall of the tide in summer is 2·4 feet. On short runs additional samples were sometimes taken at depths of 6 and 18 feet. Although samples of plankton from immediately above the bottom could not be taken successfully during the present investigation, the method devised by Carriker (1951) for avoiding the uptake of sand, mud, and other detritus with the water sample might well be utilized in future operations of this kind.

Identification and Enumeration of Plankton

The plankton was placed in a ruled Syracuse watch glass for identification and counting. Total counts were made on samples containing less than a thousand organisms. Aliquot portions were taken of well-mixed samples that were badly fouled with algæ and obscuring detritus, or contained numbers larger than one thousand. Fractionation of the 125-litre sample introduced into the estimation of total plankton content an error that increased inversely with the size of the subsample. For instance, the error for a subsample only one-eighth the size of the original sample was 15 to 20 per cent. In only a few instances, however, was it necessary to take less than one-quarter of the total sample in the counting of the larvæ, so that the subsampling error in most cases was less than 10 per cent. Counting was done under the lowest magnification consistent with accurate identification (usually 16x). The consistency of the results indicates that errors arising from methods of sampling and counting do not obscure the true picture of plankton distribution and abundance.

OBSERVATIONS

Occurrence of Adult Barnacles in the Miramichi Estuary

Three species of acorn barnacles, *Balanus balanoides* L., *B. crenatus* Brug., and *B. improvisus* Dar., are commonly found attached to rocks, stones, shells, pilings, and other suitable substrata within the limits of the Miramichi estuary. A fourth species, *Balanus balanus* L., is widespread in the Gulf of St. Lawrence but is scarce in the Miramichi area. The distribution and abundance of the three most common species in the estuary in August, 1950, were determined by means of dredge hauls and shore collections and are shown in Figure 4 and Table II.

Balanus balanoides, a species of the tidal zone, was taken mainly along the shoreline. It occurred in small numbers round the outer fringe of the estuary and was most numerous (more than ten specimens per large boulder) near Neguac on the north side, and Escuminac Point on the south side. The extreme landward penetration of the species was 10 miles above the mouth on the north side and 5 or 6 miles on the south side.

B. crenatus occurred mainly in the Gulf and outer estuary in numbers between one hundred and a thousand per standard haul. Concentrations of more than a thousand per haul were encountered near Neguac on the north side, and Escuminac on the south side. The extreme landward penetration (less than ten per haul) reached Middle Island, 20 miles above the mouth.

B. improvisus was taken in numbers greater than ten thousand per standard haul in the lower river, towards the head and south side of the bay, and near Neguac. Near the mouth of the bay, out in the Gulf, and upriver near Newcastle, the numbers were less than a thousand per haul. The extreme landward penetration (less than one hundred per haul) reached Cassilis, nearly 40 miles above the mouth of the estuary. The average density of the adult population in the area below Newcastle to the mouth may be estimated at about five thousand per standard haul which samples 600 square feet of bottom.

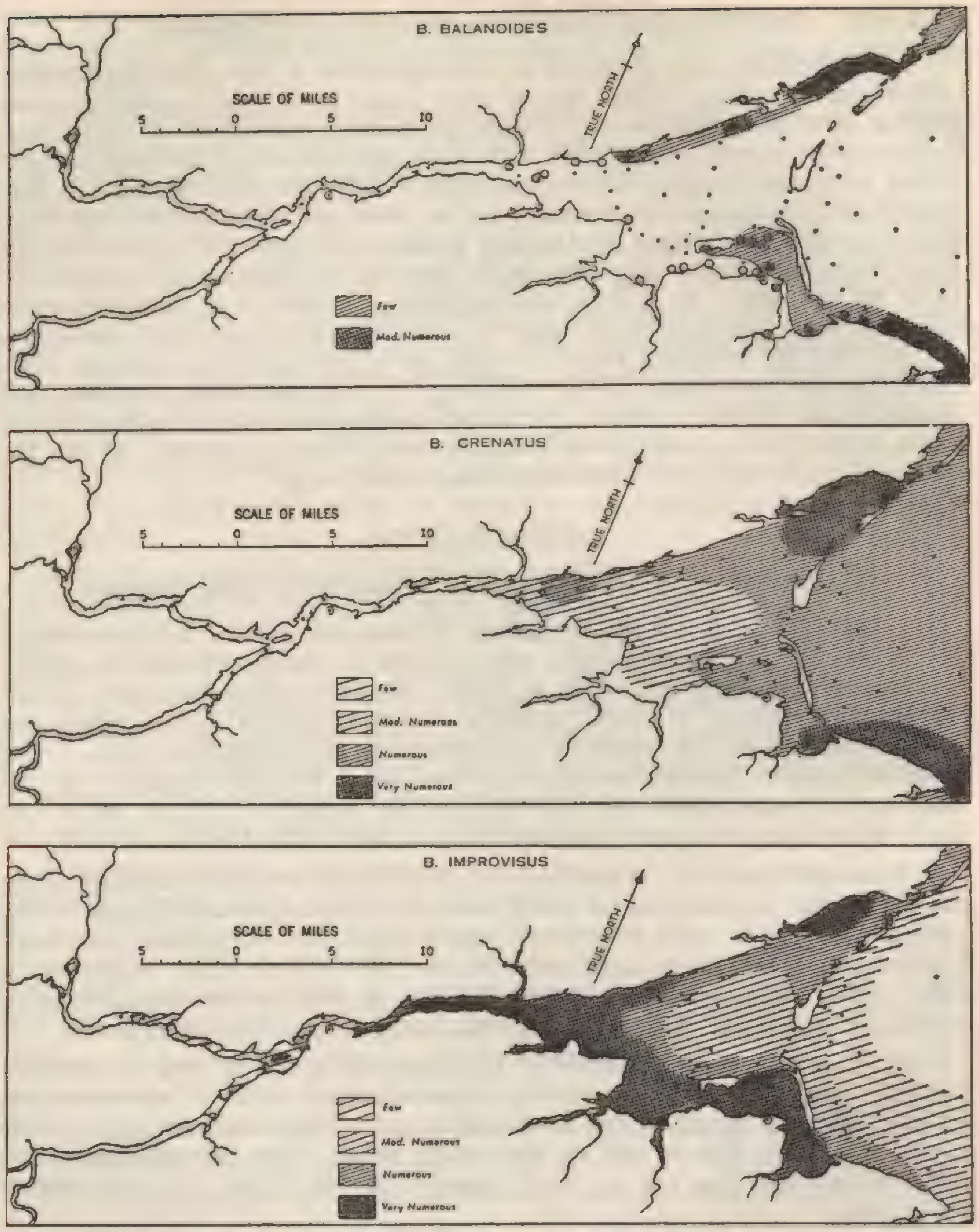

Figure 4. Distribution and relative abundance of the principal species of barnacles in the Miramichi estuary, August, 1950.

During the summer of 1951 the distributions of these species were determined in similar fashion, and wooden test panels on poles (Figure 3) were employed to obtain the set of the year. The distribution of both *B. balanoides* and *B. improvisus* in 1951 was found to be different from that of 1950. These differences appear to be correlated with the unusually heavy precipitation and river discharge during the spring and summer of 1951.

In 1951 the landward limit of adults of *B. balanoides* along the north shore was 4 miles seaward of that of 1950, and on the south side it was 2 miles seaward of the 1950 limit. Also, the upriver limit of year-old adults of *B. improvisus* in 1951 was at Newcastle, nearly 3 miles seaward of the equivalent limit in 1950. Each year, complete mortality of the most landward portion of the population of *B. improvisus* takes place, presumably because of prolonged exposure of the animals to fresh water during the spring freshets. The unusually heavy run-off in the spring of 1951 was accompanied by a mortality of all barnacles between Newcastle and Cassilis, more than 10 miles upriver, in which area they had attached in moderate numbers in 1950.

TABLE III

The horizontal vertical distribution of the 1951 year class of *Balanus improvisus* along the main river channel as shown by attachment on poles and test panels set out June 27-29, 1951

Locality	Station	Miles above mouth	Date of final examination of collectors	Depth test panel (ft.)	Number of barnacles	Depth on pole (ft.)	Number of barnacles per inch strip
Bon Ami Point.....	M14	36·5	Aug. 24	1	0	0	0
				3	0	2	0
				5	0	4	0
						6	0
Stewart Brook.....	M18	33·9	Aug. 24	....	....	0	0
				1	0	2	0
				3	0	4	0
				5	0	6	0
Boishebert Pt., SW. Miramichi.......	M38	30·6	Aug. 9	....	....	0	0
				1	0	2	0
				3	0	4	1
				5	0	6	0
Boishebert Pt., NW. Miramichi.......	M20	30·6	Aug. 24	....	....	0	0
				1	0	2	1
				3	0	4	4
				5	1	6	—
White House Farm.	M57	26·5	Aug. 31	....	....	0	0
				1	1	2	9
				3	12	4	16
				5	15	6	22
						8	29

The results of test panels in the river above Newcastle (Table III) indicate that a heavy mortality of newly attached *B. improvisus* resulted from heavy freshets in mid-July of 1951. A small number of newly attached barnacles had been observed on test panels at stations M14 and M18 on July 11. These were not seen, however, when the panels were re-examined one week following the heavy run-off of July 12 to 16 and on subsequent dates. The freshets during that period have been partly responsible for the scarcity of barnacles near the surface on such poles as they did attach (i.e. at M57). Also in 1951 the abundance of the new set of barnacles between Loggieville and Chatham, 18 to 24 miles above the mouth, was sparse, whereas in 1950, when run-off all summer long was low, the new set had been very abundant in this region.

The comparative salinity tolerances of the three species of barnacles may be illustrated by the extremes of salinity to which the adult animals were exposed during the summer of 1951. The observations on salinity are discussed elsewhere (Bousfield, 1955). For the present purpose the distribution of salinity along the main channel at surface and bottom (24 feet) for two extreme conditions of river flow during the period is given in Figure 5. The most landward specimens of *B. improvisus* and *B. crenatus* were in deepest water and exposed to bottom salinities, whereas those of *B. balanoides* were on the shore and were exposed to surface salinities

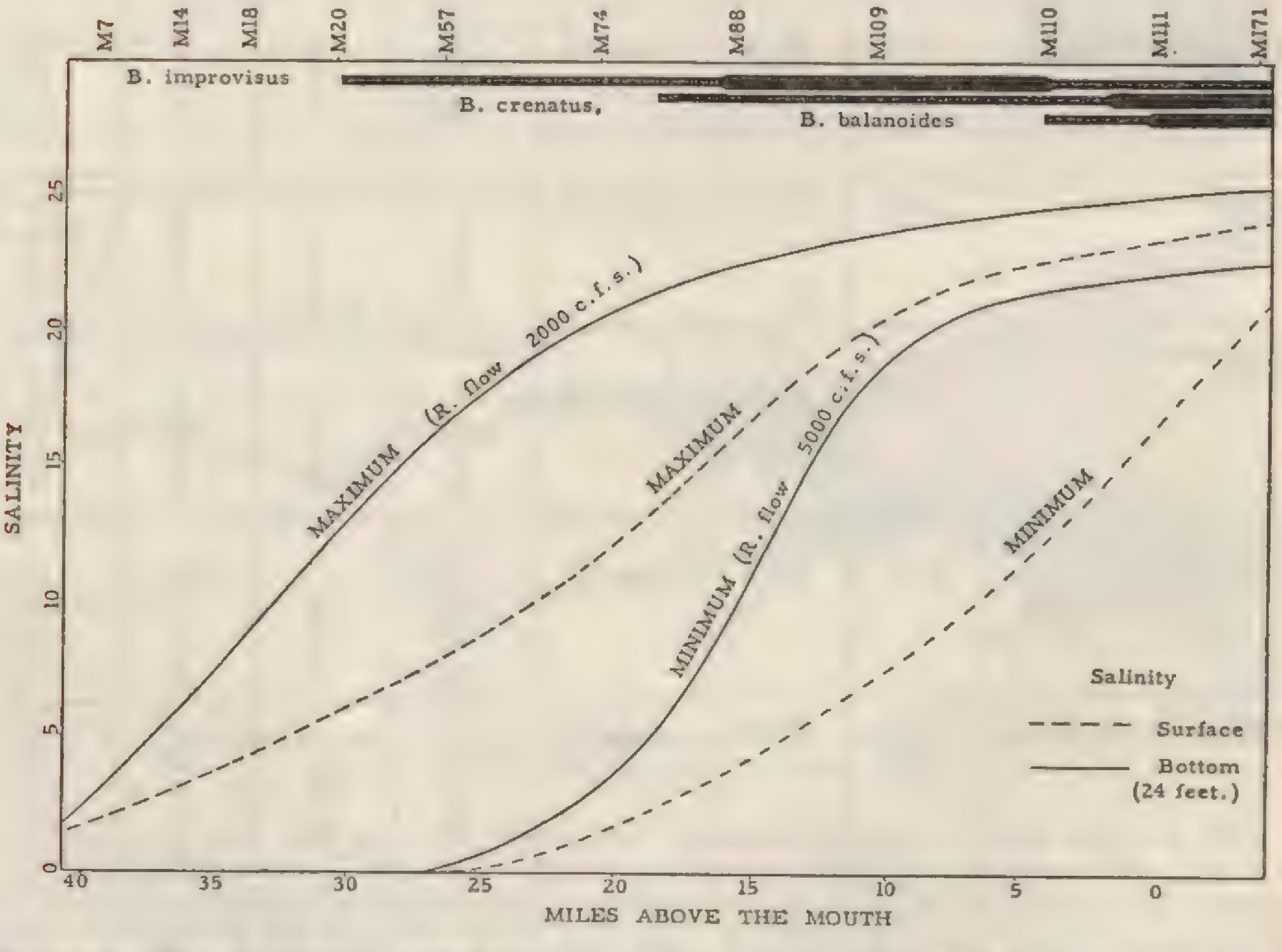

Figure 5. The distribution of *Balanus* spp. in August, 1951, and the maximum and minimum salinities at surface and bottom during June, July, and August, 1951.

The data indicate that *B. improvisus* is the most tolerant of fresh water, and *B. balanoides* the least. The most landward specimens of *B. improvisus* tolerated a range of salinity between 0 and 13 ‰; those of *B. crenatus* between 6 and 21 ‰; and those of *B. balanoides* between 12 and 23 ‰.

The range of salinity at any location is much greater during the June-August period (long-term fluctuation) than during a tidal cycle (short-term fluctuation). The summer range in all three instances above was between 10 and 15 ‰. For any given depth at the same localities, the difference in salinity between high and low water was seldom more than 5 ‰. Barnacles may close up during short periods of lethal low salinities but feed and respire when salinities are higher (i.e. at high water). Prolonged lethal low salinities thus probably set the upriver limits of distribution of the adult barnacles.

The distribution of barnacles along the main channel of the estuary in August, 1950, may be compared with that of other well-known benthic animals occurring in the Miramichi estuary (Table IV). The distributions were determined mainly from the results of dredgings and shore collections designed primarily for the sampling of barnacle populations. Those of *Rhithropanopeus*, *Teredo*, and copepods corroborate those determined in the area by Connolly (1925), M'Gonigle (1925), and Willey (1923), respectively. The distributions of *B. balanoides* and *B. crenatus* are similar to those of marine species that are most abundant in the Gulf (salinities 27 ‰) but penetrate various distances into the estuary (i.e. *Littorina* spp., *Calliopius*, *Cancer*, *Homarus*). The distribution of *B. improvisus*, however, resembles that of brackish-water species which are most abundant in the estuary proper (salinities 27 ‰) but occur sparsely in the Gulf and not at all in permanently fresh water (i.e. *Crassostrea*, *Rhithropanopeus*, *Modiolus*).

Occurrence of Barnacle Larvæ in the Estuary

Horizontal Distribution

During June, July, and August, 1951, the larvæ of *Balanus improvisus* were taken abundantly in plankton tows in the Miramichi estuary, whereas those of *B. crenatus* were much less numerous, and those of *B. balanoides* almost entirely lacking. The horizontal distribution of each of the larval stages was obtained by finding the average number of larvæ per 125-litre sample, irrespective of the depth of sampling (0, 12, and 24 feet), at each of the twenty stations visited at weekly intervals during that period. As the same plankton tows were used in the calculations for all stages, differences in the distribution and abundance between stages are independent of short-term variables, such as the stage of tide and wind direction and velocity. In the case of *B. improvisus*, errors arising from differences in the seasonal distribution of the larval stages have been minimized by averaging only the samples taken during the main period of abundance of all stages, in this instance June 13 to July 29. During this period each station was visited five or six times. *B. crenatus* occurred only in June samples.

TABLE IV

The distribution of benthic marine and fresh-water invertebrates relative to the mouth of the Miramichi estuary, N.B.

	—		Matchett's Footbridge	1 mile below Redbank	Cassilis	Bon Ami Point	Stewart Brook	Boishebert I.	Newcastle	French Fort Cove	Chatham	Middle I.	Loggieville	Sheldrake I.	Cheval Point	Oak Point	Grande Dune I.	Burnt Church	Baie Ste. Anne	Portage I. Entrance	Lower Neguac	Escuminac Breakwater	Escuminac Point
	Station number..................		M 1	M 2	M 7	M 14	M 18	M 20	M 51	M 57	M 64	M 74	M 80	M 88	M 92	M 109C	M 130	M 98	M 167	M 111	M 102	M 107	M 108
	Distance above Portage I. entrance (miles)............		49·5	41·6	39·2	36·5	33·9	30·6	28·2	26·5	23·5	20·6	17·7	15·7	12·5	10·7	8·5	4·0	1·0	0	−3·0	−7·0	−11
	Approximate average..............	0 ft.	0	0	0·2	0·8	1·0	2·5	3·0	3·5	4·5	6·0	8·0	9·0	11·5	14·0	17·0	20·4	20·1	21·0	24·0	22·0	
	Summer salinity..............	24 ft.	.....	.....	.....	.....	3·0	4·0	6·5	8·0	12·5	15·0	17·5	18·5	21·0	22·0	23·0	23·0	.....	24·0	.....	25·0	
Intertidal species	Talorchestia longicornis........							x	X			x	x	X	X	x	X	X	X	X	X	X	
	Orchestia platensis............								x	x	X	X	X	X	X	X	X	X	X	X	X	X	X
	Jaera marina..................													X	X	X	X	X	X	X	X	X	X
	Littorina rudis................													X	X	X	X	X	X	X	X	X	X
	L. littorea.....................														x	X	X	X	X	X	X	X	X
	Balanus balanoides............																x	X	x	x	X	X	x
	Ephemerida (nymphs).........		X	X	X	X																	
	Physa sp......................		X	X	X	X	X																
	Trichoptera (larvæ)...........		X	X	X	X	X	x															
	Chironomidae and Tendipedidae (larvæ).........		X	X	X	X	X	X															
	Gammarus fasciatus...........		X	X	X	X	X	X	X	X	X	X		x		x							

Littoral species	Corophium insidiosum						x	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Gammarus annulatus							x	x		X	X	X	X	X	X	X	X	X	X	X	x
	Carinogammarus							x		x			X	X	X	X		X		X		
	Gammarus oceanicus												X	X	X	X	X	X	X	X	X	X
	Calliopius laeviusculus															X	X	X	X	X	X	X
	Balanus improvisus			x	x	x	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Balanus crenatus										x	X	X	X	X	X	X	X	X	X	X	X
	Mysis stenolepis								x		x			X	X	X	X	X	X	X	X	
	Rhithropanopeus harrisi						x	X	X	X	X	X	X	X	X							
	Crago septemspinosus							x	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Neopanope texana sayi												X	X	X	X	X	X	X	X		
	Homarus americanus													?	x	X	X	X	X	X	X	X
	Cancer irroratus															X	X	X	X	X	X	X
	Hydroids			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Nereis sp.						X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Polydora sp.								x	X	X	X	X	X	X	X	X	X	X	X	x	
	Asterias vulgaris											x	x		X	X	X	X	X	X	X	X
	Macoma balthica						X	X	X	X	X	X	X									
	Modiolus demissus plicatula						x	X	X	X	X	X	X	X	X		X	X				
	Crassostrea virginica							x	X	X	X	X	X	X	X	X	X	X	x	X	x	
	Mya arenaria							x		x	X	X	X	X	X	X	X	X	X	X	X	
	Saxicava arctica								x	X	X	X	X	X	X	X	X	X	X	X	X	X
	Teredo navalis									x	x	X	X	X	X	X	X	X	X	X	X	X
	Crepidula plana									x	X	X	X	X	X	X	X	X	X	X	X	
	Mytilus									x	X	X	X	X	X	X	X	X	X	X	X	X

X—found commonly. x—found occasionally.

The horizontal distribution of successive stages of *Balanus improvisus* during the main spawning period (June 13 to July 29) is shown in Figure 6. The earliest larval stages (nauplius I and II) were most abundant near the mouth of the river and on the south side of the bay. This pattern would be expected on the basis of the distribution and abundance of the spawning adults noted earlier (Figure 5). The third and fourth nauplius stages were located progressively farther seaward and mainly on the south side, and the fifth stage was near the mouth but more in the middle of the bay. Nauplius VI was located landwards of nauplius V and more on the north side, and the cyprid was most abundant back at the river mouth and along the north side.

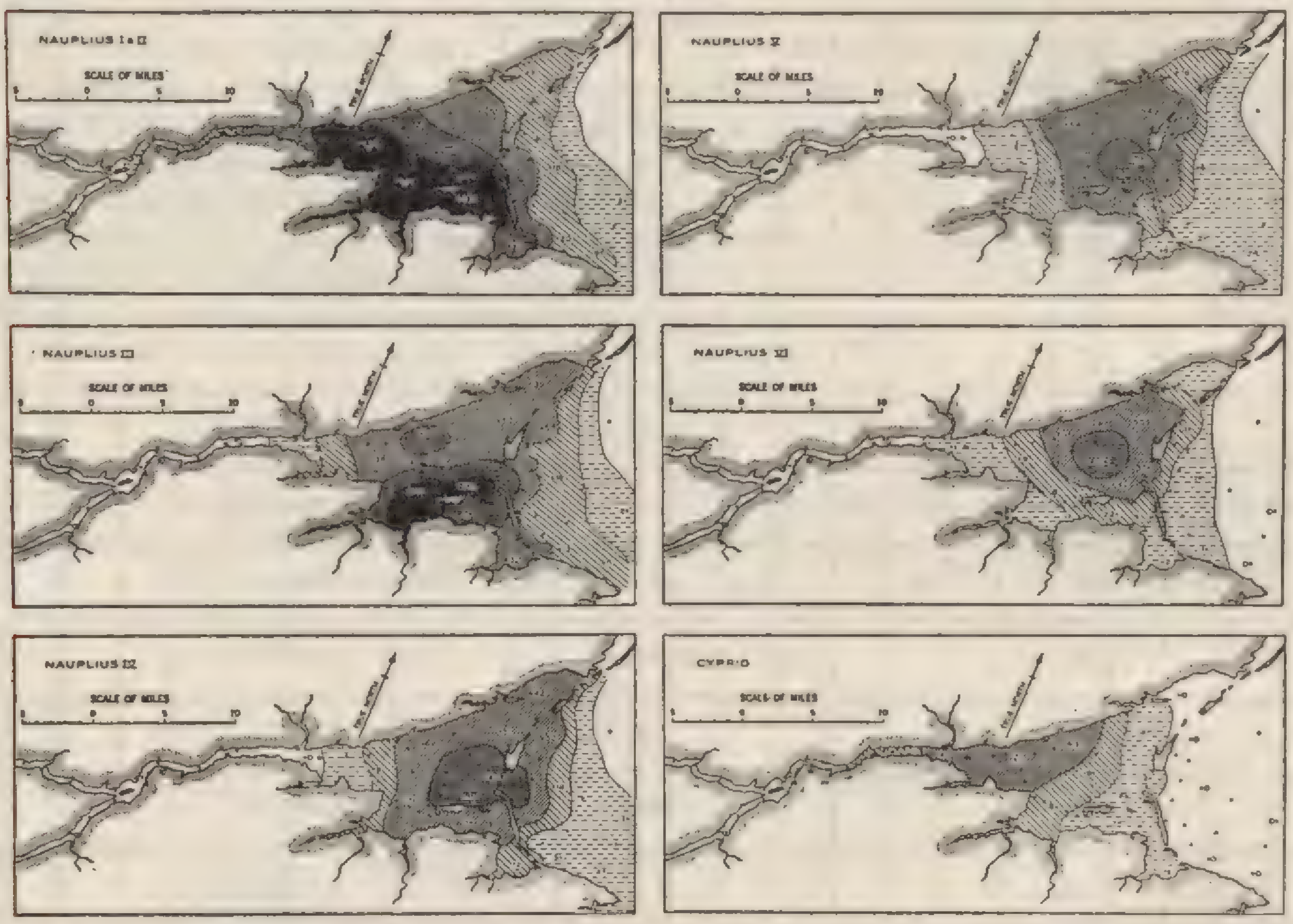

Figure 6. The distribution and abundance of larval stages of *Balanus improvisus* in the Miramichi estuary. Average number per 125-litre sample taken at depths of 0, 12, and 24 feet during June 13 to July 29, 1951.

These progressive changes in distribution indicate the net direction of movement during the entire planktonic existence of the larvæ. The movement follows an anti-clockwise ellipsoidal path over the bay portion of the estuary, first seawards along the south side, then in the middle near the mouth, and finally landwards along the north side.

Two results of this movement are notable: first, that the larval stocks, spawned in the lower river and south side of the bay, merge to form one population in the outer bay, and secondly, that the combined populations return mainly to the locality from which the river population commenced.

Movements of the larvæ of *B. crenatus,* though differing in certain respects from those of *B. improvisus,* indicate a similar tendency for greater landward transport along the north than the south side of the estuary (Figure 7). The small numbers of larvæ, particularly of late stages, taken in tows in June may not give a very accurate picture of their distribution and abundance, but do indicate changes in the degree of upriver penetration of successive larval stages.

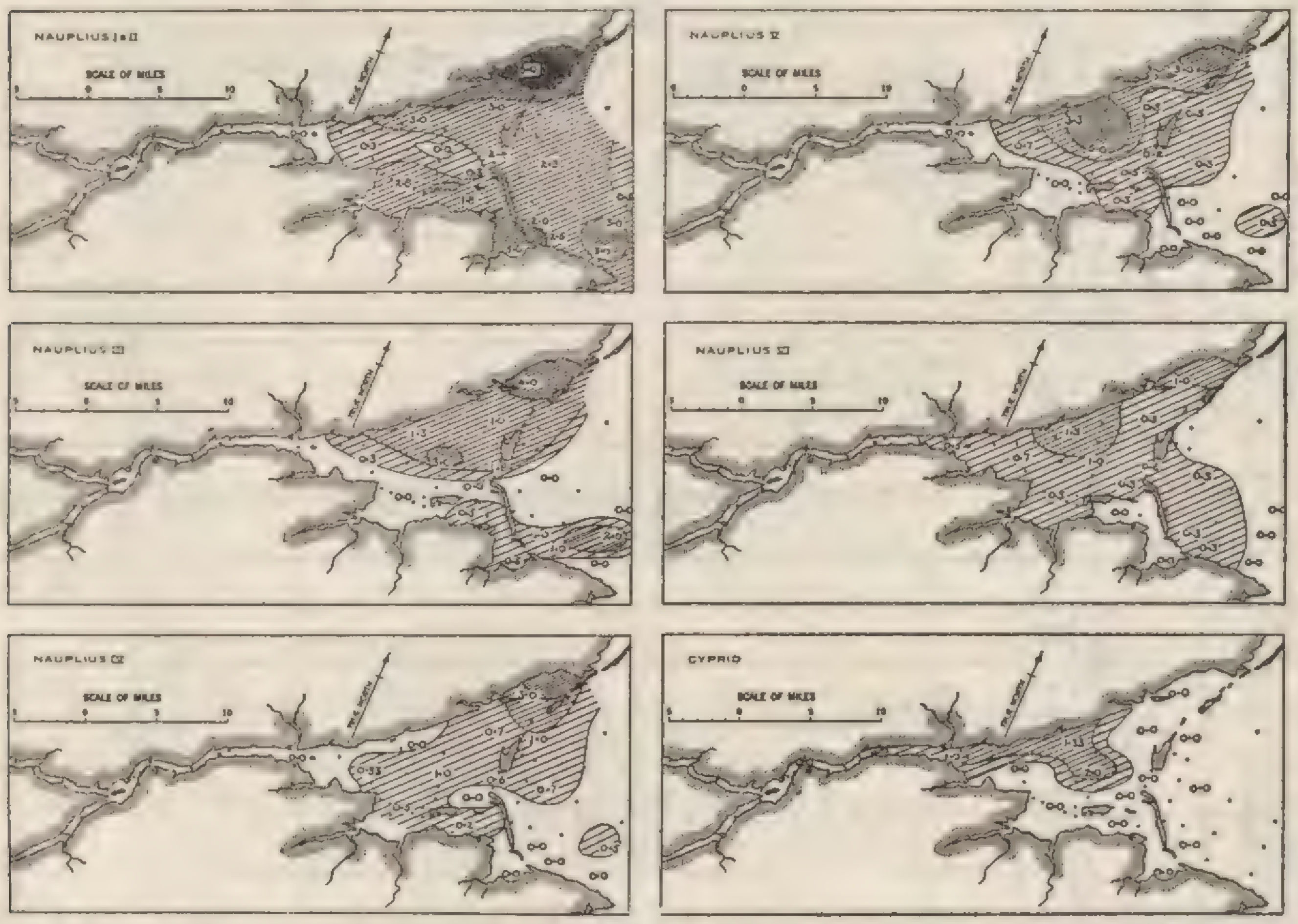

Figure 7. The distribution of larval stages of *Balanus crenatus* in the Miramichi estuary, June, 1951 (Average number of larvæ per station, all depths combined).

Two distinct populations of early stage larvæ of *B. crenatus* were present in the outer estuary; one was centred at Neguac and the other in Baie Ste. Anne. On developing to nauplius stage IV, the Neguac larvæ moved progressively towards the head, mainly along the north side of the bay, but the Ste. Anne population disappeared almost completely, evidently in a seaward direction.

The net movement of the larvæ of both species of barnacles, some seaward on the south side and some landward on the north side of the estuary, appears to coincide with the double movement of water, seaward near the surface and landward near the bottom, and with the effect of the earth's rotation on the circulation predicted elsewhere (Bousfield, 1955). These larval movements suggest that part of their existence is spent in the seaward flowing surface water, and part in the landward flowing bottom water. The influence of the circulation on these movements must therefore be explained on the basis of the vertical distribution of the larvæ.

TABLE V

The distribution and abundance[1] of larval stages of *B. improvisus* at stations along the main channel of the Miramichi estuary, weekly during June, 1951

Nauplius stage	Depth	June 5		June 2				June 3		Depth	June 13			June 17				
		Station		Station				Station			Station			Station				
	(ft.)	M57	M74	M88	M115	M110	M111	M171	M170	(ft.)	M57	M74	M88	M109	M127	M111	M171	M170
I and II	0	0	0	6	1,088	—	24	16	4	0	2	26	61	1,596	152	92	—	—
	6	4	0	149	—	—	—	—	—	6	—	—	3,092	1,016	—	76	—	—
	12	—	—	0	8	—	—	—	0	12	4	171	157	424	180	92	—	—
	18	2	2	3	—	—	—	—	—	18	—	—	9	—	184	76	—	—
	24	—	—	3	—	—	84	0	0	24	6	0	0	—	—	—	—	—
III	0	0	0	0	117	—	9	0	0	0	0	0	0	322	608	42	—	—
	6			1	—	—	—			6	—	—	4	306	—	56	—	—
	12			0	2	—	—			12	0	2	1	194	428	342	—	—
	18			0	—	—	—			18	—	—	0	—	284	192	—	—
	24			0	—	—	26			24	1	0	0	—	—	—	—	—
IV	0	0	0	0	12	—	1	0	0	0	0	0	0	64	552	20	—	—
	6	0			—	—	—			6				72	—	60	—	—
	12	—			0	—	—			12				50	170	372	—	—
	18	1			—	—	—			18				—	164	420	—	—
	24	—			—	—	—			24				—	—	—	—	—
V	0	0	0	0	0	—	1	0	0	0	0	0	0	4	376	12	—	—
	16					—	—			6			0	10	—	40	—	—
	12					—	—			12			1	11	186	154	—	—
	18					—	—			18			1	—	244	368	—	—
	24					—	—			24			0	—	—	—	—	—
VI	0	0	0	0	0	—	0	0	0	0	0	0	0	13	388	7	—	—
	6					—				6			0	33	—	12	—	—
	12					—				12			2	11	372	72	—	—
	18					—				18			0	—	1,332	120	—	—
	24					—				24			1	—	—	—	—	—
Cyprid	0	0	0	0	0	—	0	0	0	0	0	0	0	2	4	0	—	—
	6					—				6				4	—	1	—	—
	12					—				12				3	122	1	—	—
	18					—				18				—	178	2	—	—
	24					—				24				—	—	—	—	—

Nauplius stage	Depth	June 8		June 9				June 10		Depth	June 22			June 23			June 24	
		Station		Station				Station			Station			Station			Station	
	(ft.)	M57	M74	M88	M109	M110	M111	M171	M170	(ft.)	M57	M74	M88	M109	M110	M111	M171	M170
I and II	0	0	—	—	190	756	90	5	—	0	0	56	624	334	40	92	12	1
	6	0	—	—	—	36	530	—	—	6	—	—	—	—	44	—	—	—
	12	—	—	—	5	8	88	61	—	12	16	76	366	12	48	46	92	3
	18	4	—	—	—	12	69	—	—	18	—	—	—	—	160	—	—	12
	24	—	—	—	—	—	—	10	—	24	24	12	26	—	—	38	—	—
III	0	0	—	—	3	176	26	0	—	0	0	0	4	9	66	81	10	3
	6		—	—	—	24	138	—	—	6	—	—	—	—	144	—	—	—
	12		—	—	1	22	30	26	—	12	1	4	6	3	132	66	72	3
	18		—	—	—	8	43	—	—	18	—	—	—	—	354	—	—	15
	24		—	—	—	—	—	11	—	24	0	0	0	—	—	78	—	—
IV	0	0	—	—	1	108	4	2	—	0	0	0	2	3	80	14	4	0
	6		—	—	—	40	54	—	—	6		—	—	—	360	—	—	—
	12		—	—	3	22	14	4	—	12		4	0	4	212	84	76	1
	18		—	—	—	6	8	—	—	18		—	—	—	328	—	—	8
	24		—	—	—	—	—	7	—	24		0	0	—	—	90	—	—
V	0	0	—	—	2	24	1	1	—	0	0	0	0	0	48	6	2	0
	6		—	—	—	24	6	—	—	6			—	—	200	—	—	—
	12		—	—	23	4	6	1	—	12			1	3	156	34	20	3
	18		—	—	—	4	2	—	—	18			—	—	212	—	—	0
	24		—	—	—	—	—	2	—	24			0	—	—	68	—	—
VI	0	0	—	—	0	0	0	0	—	0	0	0	0	0	24	2	0	0
	6		—	—	—	1			—	6		—	—	—	296	—	—	—
	12		—	—	3	0			—	12		0	0	3	284	10	1	2
	18		—	—	—	0			—	18		—	—	—	288	—	—	0
	24		—	—	—	—			—	24		2	2	—	—	38	—	—
Cyprid	0	0	—	—	0	0	0	0	—	0	0	1	44	7	8	2	0	0
	6		—	—	—				—	6	—	—	—	—	7	—	—	—
	12		—	—	1				—	12	2	109	143	184	5	0	2	0
	18		—	—	—				—	18	—	—	—	—	29	—	—	0
	24		—	—	—				—	24	3	50	255	—	—	2	—	—

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[1] *Abundance*—numbers of larvæ per 125-litre sample.

TABLE VI

The distribution and abundance[1] of larval stages of *B. improvisus* at stations along the main channel of the Miramichi estuary, July-August, 1951

Nauplius stage	Depth	July 11			July 7			July 8		Depth	July 25			July 28			July 29	
		Station			Station			Station			Station			Station			Station	
	(ft.)	M57	M74	M88	M109	M110	M111	M171	M170	(ft.)	M57	M74	M88	M109	M110	M111	M171	M170
I and II	0 6 12 18 24	0	36 — 0 — 0	13 — 0 — 0	308 — 1 — 17	10 — 8 — 1	2 — 4 — 8	— — 0 — —	4 — — — 1	0 6 12 18 24	0	3 — 0 — 0	45 — 0 — 2	116 — 1 — 0	5 — 1 — 0	34 — — — 5	3 — 0 — —	0
III	0 6 12 18 24	0	0	0	38 — 2 — 5	26 — 20 — 1	1 — 4 — 8	— — 2 — 0	3 — 2 — 0	0 6 12 18 24	0	0	0	1 — 0 — 0	6 — 0 — —	10 — — — 2	9 — — — 0	0
IV	0 6 12 18 24	0	0	0 — 0 — 1	5 — 1 — 1	35 — 204 — 15	3 — 34 — 64	— — 4 — 0	0	0 6 12 18 24	0	0	0	0	1 — 1 — —	2 — — — —	5 — — — 0	0
V	0 6 12 18 24	0	0	0	0 — 2 — 0	12 — 296 — 25	4 — 36 — 152	— — 2 — —	2 — 0 — 1	0 6 12 18 24	0	0	0	0	1 — 3 — 3	3 — — — 3	3 — 0 — —	0
VI	0 6 12 18 24	0	0 — 0 — 1	0 — 0 — 2	0 — 12 — 2	3 — 152 — 13	0 — 12 — 76	— — 0 — —	0	0 6 12 18 24	0	0	0	2 — 0 — 0	4 — 1 — —	7 — — — 2	1 — 0 — —	0
Cyprid	0 6 12 18 24	0 — 3 — 8	0 — 8 — 16	0 — 1 — 10	1 — 15 — 15	0 — 4 — 23	— 0	0	0	0 6 12 18 24	0	2 — 48 — 16	2 — 57 — 56	2 — 1 — 39	1 — 3 — —	0	0	0

Nauplius stage	Depth	July 18			July 16			July 17		Depth	August 8			August 7				
		Station			Station			Station			Station			Station				
	(ft.)	M57	M74	M88	M109	M110	M111	M171	M170	(ft.)	M57	M74	M88	M109	M110	M111	M171	M170
I and II	0	0	0	23	57	27	2	0	—	0	1	10	137	5	6	—	—	—
	6			—	—	—	—	—	—	6	—	—	—	—	—	—	—	—
	12			2	10	2	2	4	—	12	0	1	35	0	35	—	—	—
	18			—	—	0	—	0	—	18	—	—	—	—	—	—	—	—
	24			0	4	—	4	—	—	24	0	1	0	6	48	—	—	—
III	0	0	3	2	2	2	20	0	—	0	0	0	0	1	16	—	—	—
	6		—	—	—	—	—	—	—	6	—	—	—	—	—	—	—	—
	12		0	0	6	0	4	0	—	12	2	0	0	1	38	—	—	—
	18		—	—	—	0	—	0	—	18	—	—	—	—	—	—	—	—
	24		0	0	1	—	20	—	—	24	0	0	0	5	83	—	—	—
IV	0	0	0	0	1	5	18	4	—	0	0	0	0	0	2	—	—	—
	6				—	—	—	—	—	6				—	—	—	—	—
	12				0	1	18	4	—	12				0	7	0	—	—
	18				—	0	—	3	—	18				—	—	—	—	—
	24				0	—	36	—	—	24				1	49	—	—	—
V	0	0	0	0	0	1	13	8	—	0	0	0	0	0	0	—	—	—
	6					—	—	—	—	6					—	—	—	—
	12					0	24	8	—	12					4	—	—	—
	18					0	—	2	—	18					—	—	—	—
	24					—	124	—	—	24					26	—	—	—
VI	0	0	0	1	0	1	9	0	—	0	0	0	0	0	0	—	—	—
	6			—	—	—	—	—	—	6					—	—	—	—
	12			0	0	1	14	0	—	12					0	—	—	—
	18			—	—	0	—	3	—	18					—	—	—	—
	24			0	1	—	168	—	—	24					3	—	—	—
Cyprid	0	0	0	0	0	8	4	0	—	0	0	0	0	0	0	—	—	—
	6			—	—	—	—	—	—	6					—	—	—	—
	12			1	4	4	2	0	—	12					0	—	—	—
	18			—	—	10	—	1	—	18					—	—	—	—
	24			2	7	—	2	—	—	24					1	—	—	—

[1] *Abundance*—numbers of larvæ per 125-litre sample.

Fluctuations in Horizontal Distribution

The pattern of horizontal distribution of larval stages of *B. improvisus*, previously described on page 40, was maintained during periods of relatively constant river flow but changed significantly following marked changes in precipitation and river discharge. To illustrate this point the distribution of the larvæ along the main channel of the estuary at weekly intervals during June and July is presented in Tables V and VI. During June precipitation was about normal for the month, and sudden scale changes in river discharge did not occur (Figure 5, Bousfield, 1955). A heavy run-off took place from July 11 to 29 but decreased to normal late in the month and remained so during August.

In June, with transport factors normal, nauplius I and II were most abundant at the mouth of the river (M88 and M109C), nauplius III seaward to M110, nauplius IV and V still farther seaward at M110 and M111, nauplius VI again at M109C, and the cyprid at the head of the bay and upriver even beyond Newcastle (Table V). On July 16 to 18, following a week of heavy precipitation, all stages had been displaced seawards a distance of more than 5 miles on the average (Table VI). Nauplius I and II were mainly out in the bay at M109C and M110; nauplius III had reached M111 in numbers; and whereas nauplius IV, V, and VI were located at the main entrance (M111), many more were taken out in the Gulf (M171 and M170) than usual, and the cyprids were located mainly in the bay and barely reached the mouth of the river (M88). By July 28, following a decrease in magnitude of river run-off and increase in upriver movement of salt water, the distribution of the larvæ (particularly the cyprid stage) was again similar to that of early July. By August 8, following further reductions in river discharge, the population had been displaced still farther landward. Although few larvæ were taken thereafter, this distribution remained fairly constant for the balance of the month.

All these changes in the location of the larvæ indicate that the horizontal (seaward and landward) displacement of the population varies directly with the amount and duration of the river discharge. Similarly, seasonal variations in river discharge may be shown to contribute to interspecific differences in larval distribution and to intraspecific differences in the distribution of the adults (See discussion, page 59).

Distribution of Barnacle Larvæ in Relation to Salinity

Salinity is probably the chief factor affecting the upriver limit of survival of barnacle larvæ in the Miramichi estuary. The larvæ are exposed to wide and rapid changes in salinity owing to the mixing action of the tides on fresh and salt water, and to their swimming behaviour in response to light. For instance, newly spawned larvæ at river stations M74 and M88 must pass through a vertical salinity gradient of more than 10 ‰ during their initial journey from the bottom (25 feet) to the surface.

The salinity of the water samples from which the larvæ were taken permits a comparison of salinity tolerance between stages and between species. The average number of larvæ of each stage of *B. improvisus*

TABLE VII

The average number of larvæ of *Balanus improvisus* per 125-litre sample in relation to the salinity of the water.

			Salinity (‰)																											
			0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Number of plankton-tows			49	35	20	14	5	15	12	8	6	8	10	11	5	5	16	5	12	5	20	21	32	42	42	28	34	22	26	7
Larval stage	Nauplius	I and II	0·3	6·6	0·7	1·2	6·2	6·6	8·3	32	194	442	2·8	110	173	*587*	184	199	329	102	82	321	188	92	34	21	22	25	8·3	0·7
		III	0·0	1·8	0·2	0	0	1·3	1·7	3·8	21	15	0	4·4	103	126	69	45	*239*	8·8	78	99	125	113	47	19	44	46	20	0·1
		IV	0·0	0·1	0	0	0	0	0	0·1	2·0	4·0	0	0·4	30	27	30	18	115	5·0	43	37	106	*191*	49	28	43	59	19	0·1
		V	0	0·0	0	0	0	0	0	0	0·2	2·4	0	0	3·4	2·8	17	7·2	40	3·6	19	18	69	*253*	38	24	43	42	13	0
		VI	0	0	0	0	0	0·1	0	0	0	1·8	0	0	0·4	9·2	13	2·2	38	2·6	4·2	9·2	30	*56*	44	16	19	15	1·8	0
	Cyprid		0	0·1	0·1	0	0·4	0·3	0·4	0·3	0·2	2·0	5·1	10	2·8	3·0	4·9	33	5·3	*55*	7·7	4·4	7·9	11	11	2·2	2·6	0·3	0·1	0

per 125-litre sample per unit is given in Table VII.[1] By inspection the following values of salinity were determined and summarized in Table VIII.

In *Balanus improvisus* the modal salinities were lowest for early nauplii, higher for later nauplii, and lower again for the cyprid. The extreme range of salinity tolerance was widest for early nauplii and cyprid stages and narrowest for nauplius V. The normal range of salinity was widest for nauplius III and narrowest for nauplius V. Experimental evidence might determine whether these values indicate a real difference between larval stages in the tolerance of low salinities; greatest in the early nauplius and cyprid stages and least in later nauplius stages; or whether they merely reflect the effect of seaward transport of later nauplii by the circulation (page 26). However, the data do show the range of salinities in which the larvæ will develop.

The extreme low limits of salinity tolerance in larvæ of *B. improvisus* are similar to those of the adults (Figure 5). The minimum range of salinity in which all stages occurred was 0 to 8 ‰, and in which all stages normally occurred was 8 to 16 ‰ (Table VIII). Thus the larvæ may develop normally from nauplius I to the cyprid stage in salinities that are never greater than 16 ‰ and that may reach as low as 0 ‰. The adult survives in salinities never greater than 13 ‰ during the same period of the year when all other conditions are similar to those in which the larvæ exist. Also, the modal salinity of the cyprid is 17 ‰, a value approximately equal to the average summer salinity in the part of the estuary where adult *B. improvisus* were most numerous (Figure 5).

TABLE VIII

Observed salinities in which barnacle larvæ were found.

—	Category of salinity	Larval stage					
Species	(‰)	I and II	III	IV	V	VI	Cyprid
Balanus improvisus	Mode	13	16	21	21	21	17
	Normal range	8–21	9–25	12–25	16–25	13–25	10–22
	Extreme range	0–27	0–27	1–27	8–26	5–26	1–26
Balanus crenatus	Mode	21	20	24	20	19	15
	Normal range	16–27	15–27	—	—	—	—
	Extreme range	8–27	8–27	8–27	15–27	15–26	10–24

the mode—salinity value with the greatest number of larvæ
normal range—values within which 95 per cent of the larvæ were taken
extreme range—values within which the larvæ occurred

The larvæ of *B. crenatus* occurred in somewhat higher salinities than those of *B. improvisus,* but the data are less significant owing to the small numbers of larvæ of the former species taken. Early nauplii occurred mainly in salinities greater than 20 ‰ and nauplius VI and the cyprid mainly in salinities of 19 and 15 ‰, respectively. Spawning adults were located in the Gulf and outer bay where salinities were relatively high, and newly-spawned larvæ were therefore taken in comparably high salinities.

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[1] The unusually low numbers of larvæ taken in 10 ‰ may be attributed to the fact that nine of the ten stations in this category occurred prior to June 6 and later than July 25, outside the main spawning season.

The range of salinities for the larvæ of *B. balanoides* could not be observed. As the larvæ are restricted to the mouths of the estuaries (page 19), the range of salinities was probably much as in *B. crenatus.*

Comparison with Other Miramichi Zooplankton

The distribution of the larvæ of *Balanus improvisus* along the main channel of the estuary may be compared with that of other zooplankton organisms occurring in the Miramichi estuary (Table IX). The distributions were determined from the results of plankton samples taken during June, July, and August, 1951. The distribution of *B. improvisus* is similar to that of brackish-water forms that are most abundant inside the estuary but occur only in relatively small numbers in the Gulf and in fresh water near the head of the estuary (i.e. the copepods *Eurytemora hirundoides* and *Acartia tonsa,* and the larvæ of the mud crab *Rhithropanopeus harrisii*).

The distribution of the larvæ of *B. crenatus* (not shown) is similar to that of the arrow worm *Sagitta elegans* which originates in the Gulf, penetrates the outer estuary in small numbers, and becomes concentrated in the deeper parts of the channel some distance above the mouth.

Vertical Distribution

The average daytime vertical distribution of the larval stages of the three species of barnacles in the Miramichi estuary has been calculated from the results of weekly plankton pump hauls at ten stations in the Bay at depths of 0, 6, 12, 18, and 24 feet (in the channel) during June, July, and August, 1951 (Figure 8). The average vertical distribution is an expression of the combined influence of larval swimming behaviour and larval transport by the water circulation. As previously noted (p. 11) the swimming behaviour may vary according to the time of day, the transparency of the water, and other factors. The vertical circulation changes with the stage of tide, wind direction and velocity, and other physical variables.

Nauplius stages I and II of *B. improvisus* were found mainly near the surface, indicating that the early stage larvæ rise from the bottom soon after liberation from the mantle cavity of the spawning parents. The average depth above which 50 per cent of the population occurred (median depth) was 6·2 feet. The median depth of nauplius III was 7·8 feet. Nauplius IV and V were found mainly in mid-depths (11·3 and 12·0 feet respectively), whereas nauplius VI and the cyprid were closer to the bottom (14·2 and 15·4 feet respectively). Nauplius stages I to III were thus above, stages IV and V at or slightly below, and nauplius VI and the cyprid well below the level of no net motion. This level, separating the upper layer of residual seaward drift from the lower layer of landward drift, is estimated to be about 10 feet in depth in Miramichi Bay (Bousfield, 1955).

TABLE IX

The distribution of planktonic marine, brackish, and fresh-water invertebrates relative to the mouth of the Miramichi estuary, N. B.

	Station		M7	M14	M20	M57	M74	M88	M109C	M110	M111	M171	M170
	Distance above Portage I. entrance (miles)		39·2	36·5	30·6	26·5	20·6	15·7	10·7	4·2	0·0	−3·8	−9·6
	Approximate average	0 ft.	0·2	0·8	2·5	3·5	6·0	9·0	14·0	18·0	21·0	23·0	25·0
	Summer salinity	24 ft.	—	—	4·0	8·0	15·0	18·5	22·0	23·5	24·0	25·5	26·5
	Species												
Fresh-water species	Bosmina longirostrum var. cornuta		**X**	X	X	x	x	x					
	Cyclops viridis		X	X	**X**	X	X	x	x				
	Cypria sp.		X	**X**	X	x	x						
Brackish-water species	Laophonte huntsmani		X	X	X	**X**	X	X	x	x			
	Ergasilis chautauquaensis		x	x	**X**	X	X	x	x	x			
	Eurytemora hirundoides		x	X	X	X	X	**X**	X	X	x	x	
	Acartia tonsa		x	X	X	X	X	X	**X**	X	X	X	x
	Balanus improvisus (nauplius I and II)		x	x	x	x	X	**X**	X	X	X	x	x
	Rhithropanopeus harrisii (zoeae)			x	X	X	**X**	X	x	x			
	Eurytemora herdmani			x	x	x	X	X	X	**X**	X	X	X
	Acartia clausi			x	x	x	x	X	X	X	X	**X**	X
	Pseudodiaptomus coronatus				x	x	x	X	X	**X**	X	x	
	Temora longicornis				x	x	x	x	x	X	X	X	**X**
	Tortanus discaudatus				x	x	x	X	x	x	X	**X**	X

Marine species	Oithona similis			x	x	X	X	X	X	X	X	**X**
	Evadne nordmanni			x	x	x	x	X	X	**X**	X	X
	Podon leuckarti				x	x	x	X	X	X	**X**	X
	Pseudocalanus elongatus				x	x	x	X	X	X	X	**X**
	Calanus finmarchicus				x	x	x	x	x	x	X	**X**
	Sagitta elegans					x	**x**	x	x	x	x	x
	Labidocera aestiva					x	X	X	**X**	x		
	Centropages hamatus						x	x	X	X	**X**	X

Abundance (based on the average number per 125-litre sample during June, July, and August, 1951):
X—abundant; **X**—most abundant; x—relatively scarce; less than 1/10 the most abundant; **x**—scarce, even where most abundant.

The nauplius stages of *B. crenatus* were taken most abundantly at mid-depths, and deeper than corresponding stages of *B. improvisus*. The median depth of stages IV and V was about 12 feet, and similar to that of *B. improvisus*. The median depths of nauplius VI and the cyprid were 15·8 and 17·5. feet respectively. All stages of *B. crenatus* thus occurred mainly below the level of no net motion, and the very early and very late stages in particular were much deeper than corresponding stages of *B. improvisus*.

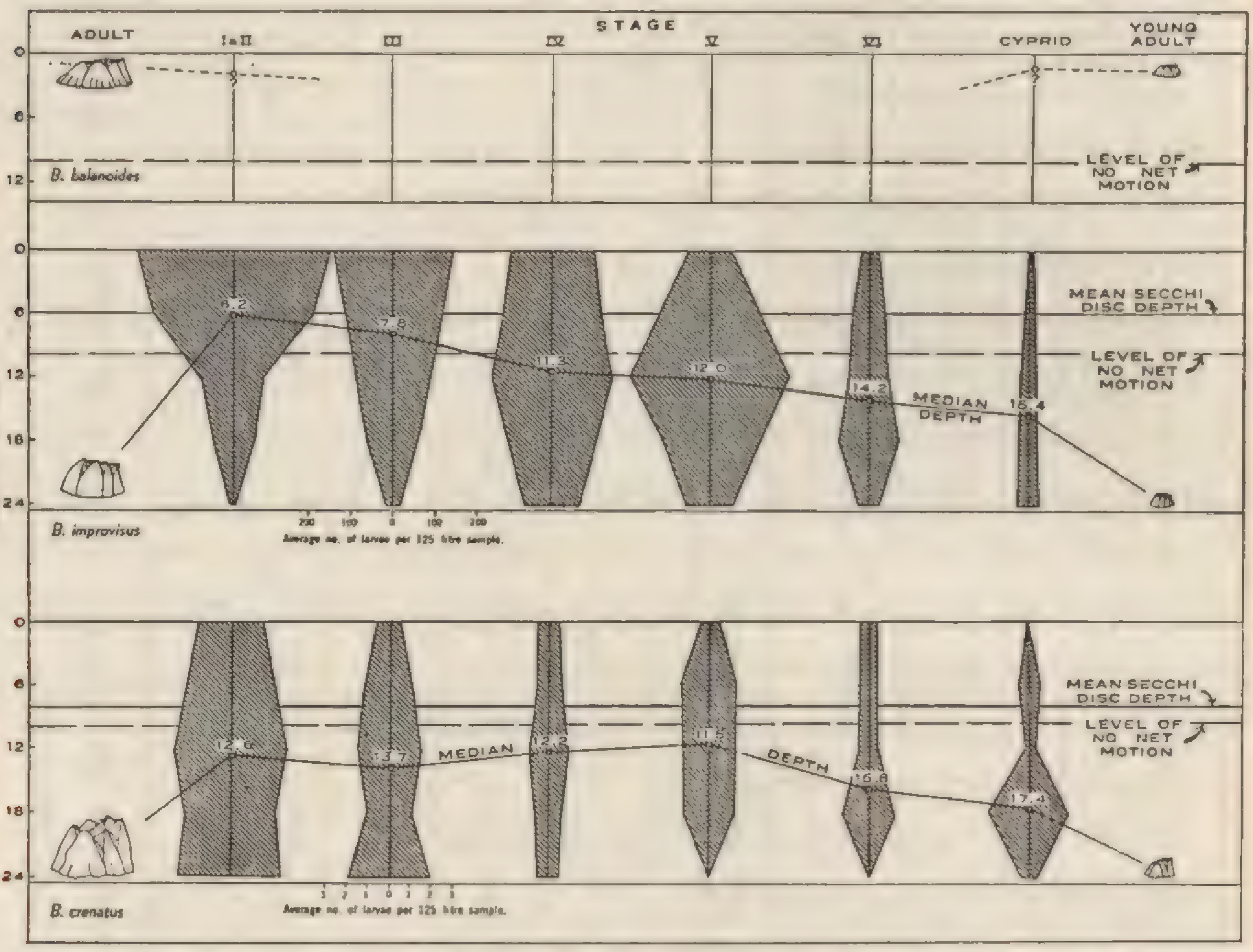

Figure 8. The average daytime vertical distribution of the larval stages of barnacles in the Miramichi estuary.

Data on the vertical distribution of the larvæ of *Balanus balonides* in the Miramichi estuary are lacking since the main spawning period was prior to the time when plankton samples were taken. The results of plankton tows taken elsewhere (Bousfield, 1954), the analysis of the vertical distribution of the adults in the tidal zone, and the results of other investigations (Bassindale, 1936; Fales, 1936; Pyefinch, 1948b) show that the early and late stage larvæ usually occur near the surface. In the Miramichi estuary these larvæ would therefore probably occur above the level of no net motion (Figure 8).

The difference in vertical distribution between species may be partly attributable to corresponding differences in the transparency of the water in which the larval species occurred. Thus the average Secchi disk value for stations at which the larvæ of *B. crenatus* occurred was 8·0 feet, that of *B. improvisus* 6·0 feet, and that of *B. balanoides* was probably still less. Moreover, the depth distribution of *B. improvisus*, based on large numbers

(100 to 200 per sample) is probably much more accurate than that of *B. crenatus,* based on small numbers (1 to 3) per sample, but in the case of *B. balanoides* Miramichi data are lacking.

Changes in Vertical Distribution with Stage of Tide

Carriker (1951) and others have shown that the vertical distribution of oyster larvæ may vary according to the stage of the tidal cycle. To determine whether the vertical distribution of the larvæ of *B. improvisus* is also influenced by the stage of tide, the data from which the average daytime distribution was derived have been regrouped on the basis of the phase of tide regardless of when the samples were collected or of the location of the station.

For simplicity the depth distribution (at a given stage of tide) may be expressed in terms of proximity to the surface and represented by the geometric mean ratio:

$$\sqrt[n]{\frac{(N_o)}{N_{12}}_1 \frac{(N_o)}{N_{12}}_2 \frac{(N_o)}{N_{12}}_3 \cdots\cdots\cdots \frac{(N_o)}{N_{12}}_n}$$

where N_0 and N_{12} are corresponding numbers of larvæ per haul at depths of 0 and 12 feet respectively, and 'n' is the number of paired samples taken at the particular stage of tide. Where the geometric mean ratio equals unity, the numbers of larvæ at surface and 12 feet are equal; where it is 10, there are ten times as many larvæ at the surface as at 12 feet; but where the ratio is only 0·5, there are twice as many larvæ at 12 feet as at the surface. The final results of these calculations have been summarized in Table X and plotted in the form of smoothed curves in Figure 9.

The changes in depth position during a complete tidal cycle, shown by nauplius stages I and II combined, are representative of the first five nauplius stages. In all cases the nauplii were located nearest the surface at high and low water but deepest down during mid-ebb and mid-flood. The nauplii were stationed higher during mid-flood than during mid-ebb. Successive stages tended to be progressively deeper down regardless of the stage of tide. The greatest surface accumulation of successive nauplius stages was reached at progressively later times during HW and LW. Nauplius VI showed a pattern of change during the falling (ebb) tide that was similar to the earlier stages, but there was no significant drop to a low level on the flood. The cyprid showed irregular changes in level throughout the tidal cycle but was nearest the surface during flood tide.

The regular changes in the vertical distribution of the larvæ may be correlated with changes in the levels of certain factors which might influence the swimming behaviour. The changes in average light intensity during the tidal cycle (Figure 9) do not follow a regular sequence paralleling those of the larvæ, however. For instance, the average sky clarity was greatest at high water and lowest at mid-ebb but was not high at low water nor low at mid-flood. Furthermore, changes in average water transparency throughout the tidal cycle (Table XI) paralleled in general those of sky clarity, except for a low value at high water. These limited data do not

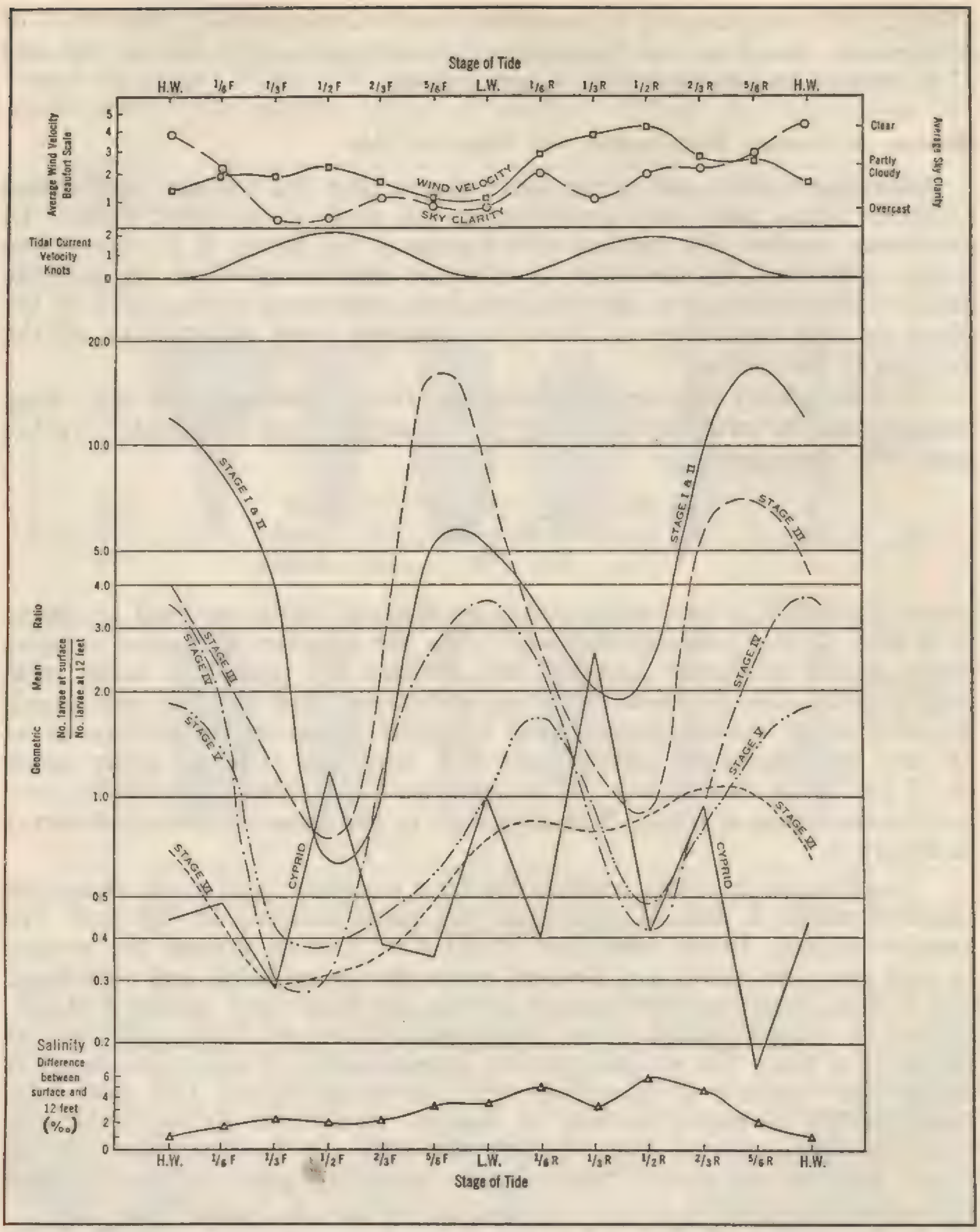

Figure 9. The average vertical distribution of larval stages of *B. improvisus* in the Miramichi estuary relative to the stage of tide, wind velocity, and current velocity.

show a relationship between changes in the total light penetration of the water and changes in the vertical distribution of the larvæ. And if changes in the magnitude of salinity gradient between surface and bottom influence larval swimming behaviour, the data of Figure 14 likewise provide no evidence. Salinity differences were greatest at mid-flood, least at high water, but showed no regular fluctuation similar to that of the larvæ.

TABLE X

The geometric mean ratio $\frac{\text{numbers at the surface}}{\text{numbers at 12 feet}}$ of the larvæ of *Balanus improvisus* in relation to the stage of tide

(Depth curves, Figure 9, are based on these data)

Larval stage	Stage of tide											
	HW	1/6F	1/3F	1/2F	2/3F	5/6F	LW	1/6R	1/3R	1/2R	2/3R	5/6R
I and II........	3·9	5·3	5·5	1·2	·90	5·4	4·8	2·9	2·6	1·8	10·1	17·1
III.............	2·3	8·0	1·8	·78	1·6	16·0	7·8	1·8	1·5	·81	6·6	6·5
IV..............	3·8	2·2	·19	·62	·54	2·7	3·7	2·5	·95	·40	·96	2·0
V...............	·33	1·5	·36	·38	·45	·62	·69	1·6	·92	·47	·93	1·3
VI..............	·15	1·7	·25	·28	·56	·23	·86	·89	·76	·82	1·1	1·0
cyprid..........	·45	·50	·28	1·2	·38	·36	1·0	·39	2·5	·40	·93	·16

The values of tidal current and wind velocity, on which the turbulence of the water depends, corresponded to those of the larval distributions during the tidal cycle (Figure 9). The net result of changes in both wind velocity and current velocity was that water movement and vertical turbulence were greatest on the rising (flood) and falling (ebb) tide but least at high and low water. The fact that the numerical value of the difference in salinity between surface and 12 feet was not minimal at mid-ebb and mid-flood does not necessarily contradict the assumption of greatest mixing at those times and least at high and low water. The values are partly attributable to the small number of stations (two to ten) used in the calculation of the average values for each stage of tide, and also to the geographical location of the stations. The numerical value of these salinity differences is greatest for river stations where vertical stratification is greatest, and least for bay stations where stratification is least. Changes in salinity with depth throughout a complete tidal cycle at station M57 (Bousfield, 1955, Figure 11) show that the instantaneous relative difference in salinity between surface and 12 feet at river stations *is* minimal at mid-ebb and mid-flood and greatest at high and low water.

TABLE XI

Average Secchi disk readings at plankton stations in the bay in relation to the stage of tide

—	Stage of tide											
	HW	1/6F	1/3F	1/2F	2/3F	5/6F	LW	1/6R	1/3R	1/2R	2/3R	5/6R
Secchi d. reading (ft.)...	5·5	7·7	6·6	6·2	7·1	5·8	7·2	?	7·5	7·1	7·0	8·4

The results of this analysis show that the vertical distribution of the larvæ of *B. improvisus* fluctuates regularly in accordance with the phase of the tidal cycle, and indicate that these changes are correlated with changes in water velocity. Vertical mixing is greatest at greatest tidal and wind velocities, and it is at these times that the numbers of larvæ of all stages are most nearly uniform from top to bottom. Early stages near the surface presumably tend to be stirred downwards and late stages near the bottom upwards by increased vertical turbulence at mid-flood and mid-ebb. The depths of the larval stages relative to each other are apparently maintained to some degree throughout the tidal cycle. The average or median depths regardless of the stage of tide calculated in Figure 8 may justifiably be used in further considerations of the influence of the circulation on the dispersal of the larvæ.

Mortality and Seaward Dispersal of Planktonic Larvæ

Observations thus far have shown that the larvæ of *B. improvisus* originate mainly near the head of the bay, circle the outer estuary during their period of planktonic existence, and reach the head of the bay again at the attachment stage. The numbers of larvæ attaining the cyprid stage are much smaller than those initially spawned owing to mortality and seaward dispersal from the estuary during the interim.

The rate of total loss of the larvæ of *B. improvisus* combines the rate of mortality from all causes with the rate of seaward loss (dispersal) from the estuary. This rate, expressed as percentage per day, may be calculated from the average decrease in abundance of the estuarine population as a whole, provided the duration of the planktonic life stages are known.

As previously noted (p. 10), the duration of larval life in *B. improvisus* was found to range from two weeks to more than a month, depending chiefly upon the locality and the temperature of the water. The duration of larval life in the Miramichi was estimated from the dates on which the earliest and latest planktonic stages first became abundant (Table XII). This period lasted more than two weeks, from June 1 to June 17, during which water temperatures were about 14 to 16°C.

The duration of the individual life stages was similarly estimated (Table XII). On June 2 and 3, nauplius II was abundant and a few nauplius III were present. Nauplius I was seldom observed in preserved plankton material owing chiefly to its rapid metamorphosis to nauplius II during the interval between the collection and preservation of the sample (p. 18) and has been included with nauplius II. On June 9, both nauplius IV and VI were abundant, and nauplius V had appeared. By June 17 nauplius V and VI had appeared in large numbers, and many late-stage nauplius VI were in the process of metamorphosing to the cyprid stage. The duration of development at 15°C. from mid-nauplius II to early cyprid may be estimated at two weeks, and the duration of each nauplius stages III to VI at about two and one half days.

The duration of nauplius II and the cyprid of *B. improvisus* cannot be estimated from the data at hand (Table XII). The duration of nauplius II in *B. balanoides, B. crenatus* (Table I), and generally in all species of barnacles is longer than that of subsequent nauplius stages. The duration of nauplius II in *B. improvisus* is thus probably longer than two and one half days and may be four or possibly five days at the prevailing temperature (15°C.).

TABLE XII

The average number of larvæ of *B. improvisus* in the Miramichi estuary per 125-litre sample at weekly intervals during the summer of 1951. Counts made on samples from depths of 0, 12, and 24 feet at 15 stations mainly in the bay.

Larval stage	Average number of larvæ per 125-litre sample													
	June 1–5	June 9–10	June 17	June 23–24	July 1–2	July 7–8	July 15–17	July* 22–23	July 28–29	Aug. 7	Aug. 13	Aug. 20	Sept. 2–3	June-July
I and II............	149·0	177·0	382	314	155·0	66·0	86·0	62·0?	63·0	33·0	7·3	1·4	3·5	190
III.................	30·0	95·0	303	157	108·0	116·0	54·0	52·0?	7·2	33·0	3·6	1·2	0·8	123
IV..................	1·4	54·0	198	89	92·0	39·0	29·0	21·0?	2·3	8·8	3·4	1·2	0·3	75
V...................	0·2	23·0	125	47	54·0	69·0	32·0	26·0?	1·8	3·8	4·3	0·7	0·0	54
VI..................	0·1	1·5	154	40	9·4	23·0	29·0	14·0?	3·2	0·4	1·0	0·5	0·1	39
Cyprid............	0·1	0·1	20	30	13·0	3·9	4·2	4·3?	9·1	0·1	0·1	0·5	0·0	12
Total...........	181·0	351·0	1,182	677	431·0	317·0	234·2	179·0?	86·0	79·0	20·0	5·5	4·7	493

*Numbers for July 22-23 (no plankton hauls made) obtained by averaging numbers for July 7-8, July 15-17, July 28-29, and Aug. 7.

The duration of the cyprid in the plankton would depend upon the availability of substrata suitable for attachment, the amount of vertical turbulence among other factors. On June 17, cyprids of *B. improvisus* first became abundant in plankton tows, but no new set was observed on buoys on that date. On June 24, however, the buoys on both north and south sides of the bay were heavily coated with newly-attached *B. improvisus*, most of which were about one millimeter in basal diameter, and thus only about two or three days old. Visscher (1928) observed a variable planktonic period in cyprids of *B. improvisus* in culture dishes, and a few attached only after a period of ten or eleven days. In the Miramichi it will be assumed that most (90 per cent) of the cyprids have attached by the end of the fourth day.

The total duration of larval existence from spawning to attachment in *B. improvisus* is estimated to be about three weeks (21 days) during early June when the water temperature was about 15°C. However, it may be little more than two weeks during July and August when surface temperatures are 19 to 20°C. At an average temperature of 17·5°C. for late June and early July, the period of maximum abundance of the larvæ, the normal duration is probably about mid-way between two and three weeks, or about eighteen days.

From all these considerations the probable durations of the larval stages of *B. improvisus* in the Miramichi estuary are estimated to be as follows:

	days
Nauplius I and II combined	4
Nauplius III to VI (2½ days each)	10
Cyprid prior to attachment	4
	18

Values more precise might be computed from life tables, provided continuous daily observations of larval development were made. For the precise determination of the rate of development under controlled temperatures, rearing of the larvæ in the laboratory would be desirable.

The rate of total loss may be computed from the standard mortality equation:

$$P_t = P_o\, e^{-kt};\ \text{or}\ l_n \frac{Pt_2}{Pt_1} = {}^{-k}\,(t_2 - t_1)$$

Derivations of the interval between successive stages and of the age of a given stage relative to initial spawning are presented in columns 3 and 4, respectively, of Table XIII. Thus at mid nauplius stage II (assumed to be 2 days old) the average number of larvæ per 125-litre sample was 190, whereas that of mid nauplius stage VI (12·75 days old) was only 39. Substituting these values in the above equation:

$$l_n \frac{39}{190} = 10{\cdot}75k$$

$$k = 0{\cdot}145$$

The rate of total loss from mid nauplius II to mid nauplius VI is therefore 14·5 per cent per day.

TABLE XIII

The average abundance of larvæ of *Balanus improvisus* at various stages of the planktonic existence, during June and July, 1951.

(water temperature 15 to 19°C.).

(1) Larval stage	(2) Estimated duration of stage (days)	(3) Interval between successive stages (days)	(4) Age relative to the initial spawning (days)	Average number of larvæ per 125-litre sample	
				(5) "Observed"	(6) "Calculated" (mortality = 14·5% per day)
Nauplius I at liberation	0		0		254
		2			
Nauplius II	4		2	190	190
		3¼			
III	2½		5¼	123	119
		2½			
IV	2½		7¾	75	83
		2½			
V	2½		10¼	54	57
		2½			
VI	2½		12¾	39	39
		1¼			
New cyprid	0		14		33
		2			
Cyprid	4		16	12	25
		2			
Metamorphosing cyprid	0		18		19
Totals	18	18	86		

If the value of 'k' predicted above is used in the mortality equation, the abundance of the larval population may be predicted for any moment, from newly liberated to the attachment stage (Table XIII, column 6). The general agreement of the "calculated" with the "observed" values through nauplius stage VI lends support to the accuracy of the estimated duration of each larval stage and to the validity of the assumption that the numbers per haul represent the abundance of the population mid-way through each life stage.

If the calculated rate of total loss continues during the cyprid stage, the number remaining after two days would be twenty-five rather than twelve as observed. This discrepancy is attributable, of course, to attachment of cyprids during that period. The rate of attachment is thus probably about 30 per cent per day.

The percentage survival of barnacle larvæ may be calculated provided the abundance of both newly liberated and attachment stage larvæ is known. The average number per sample of newly released larvæ (nauplius I) has been calculated to be 254 and that of the new cyprids, fourteen days later, to be 33 (Table XIII). Survival to the cyprid stage is therefore $^{33}/_{254}$ or 13 per cent. Allowing for a total loss of 14·5 per cent per day of cyprids still planktonic, the percentage of larvæ surviving to attachment may be conservatively estimated at about 10 per cent.

Survival of Attached Larvæ

The survival of barnacle cyprids at the time of attachment depends upon the suitability of the substratum. The scarcity of rocky outcrops, boulders, pilings, and wave resistant substrata (in the tidal zone) accounts mainly for the low numbers of successfully attached cyprids of *B. balanoides* in the tidal zone of the sandy barrier islands across the mouth of the estuary. *Balanus crenatus* survives on the sandy bottom of the Gulf and outer estuary through attachment to the shells of *Spisula, Mya, Mytilus, Crassostrea,* to other barnacles, and to the carapaces of lobsters and crabs. *Balanus improvisus* populates estuarine mud flats, an area from which it would normally be excluded, through attachment to the shells of oysters both living and dead. Indeed, its distribution closely parallels that of the principal oyster beds in the estuary (Medcof, 1943). Newly attached barnacles were found also, particularly at upriver localities, on *Mytilus, Mya, Modiolus demissus,* on small stones and pebbles, and even water-logged bark on the sandy mud bottoms. Attachment appeared to be moderately successful along the rocky Escuminac coast, but less so over the sand bottoms of the central and outer bay where bivalve shells and other suitable substrata were relatively scarce.

The distribution and abundance of *B. improvisus* in the Miramichi estuary in August, 1950, are shown in Figure 4. Dredge hauls show that the density ranged from less than 500 to more than 10,000 per standard haul sampling 600 square feet of sea bottom. The average density for the whole estuary might be placed at 5,000 barnacles per 600 square feet, or approximately one per 20 square inches. If 50 per cent of these survived until the following June (page 7), the density of spawning adults might be one per 40 square inches.

The "saturation" value of suitable bottom substrata might be placed at twenty mature adult-sized barnacles per square inch, as actually observed in crowded colonies of *B. improvisus* on buoys. From the results of dredge hauls the area of suitable substrata (shells, stones, etc.) is estimated to be equivalent to less than 5 per cent of the bottom area. Thus if all bottom substrata were "saturated" with adult *B. improvisus,* the average density would be only one barnacle per square inch of bottom. From these figures it appears that *B. improvisus* occupies less than one-twentieth of potentially good sites. Near the head and south side of the bay, the concentration was somewhat greater than this, but less out in the middle of the bay.

Whether the number of larvæ of *B. improvisus* reaching attachment stage inside the estuary would be sufficient to maintain the adult population therein may be tested in two ways. The number of attaching larvæ per adult barnacle may be estimated from the number of larvæ spawned per adult and the percentage survival previously calculated. Also, the total cyprid production during the spawning season may be computed in terms of numbers per square unit of sea bottom and compared with the observed density of the adult population.

Assuming that each mature adult barnacle produces between 1,000 and 10,000 nauplii (p. 8), the number surviving to attachment (10 per cent survival) would be 100 to 1,000. As only one of these need survive until the following year to maintain the breeding population, the numbers of larvæ retained within the estuary to attachment appear to be sufficient for this purpose.

The total cyprid production in *B. improvisus* may be calculated as follows: A population density of 39 nauplius VI per 125 litres of sea water produces 33 cyprids per equivalent volume every 2½ days (Table XIII). Assuming that the average mid-tide depth of the estuary is approximately 5 meters (16·5 feet), the number of cyprids produced during the seven-week period of abundance would be approximately 2·5 per square cm. or 17 per square inch of sea bottom. As the average number of barnacles in August, about one month after most attachment takes place, is only one per 20 square inches, the ratio of attaching cyprids to maturing adults is about 350:1, and to spawning adults 700:1, presumably adequate to maintain the breeding population.

From these figures on the density of the adult population and of surviving cyprids, the assumption that each mature adult produces between 1,000 and 10,000 nauplii is validated. Thus if the ratio of cyprids to spawning adults is 700:1 and survival of the larvæ is 10 per cent, the number of larvæ spawned per adult would be approximately 7,000. This figure is of the same order of magnitude (1,000 to 10,000) assumed above.

Plankton Dispersal and Water Movement

Dispersal of Barnacle Larvæ

Changes in the horizontal distribution of the larval stages of barnacles during their planktonic existence in the Miramichi estuary (Figures 7 and 8) are apparently determined by the vertical distribution of the larvæ in relation to the residual drift of the water.

An account of the circulation in the Miramichi estuary derived from physical factors is presented elsewhere by the writer (1955, Figures 1, 11). The principal applicable conclusions are as follows: The Miramichi is a tidal estuary of the coastal plain type, having a seasonally variable influx of fresh water at the landward end. During the summer at least, the water is vertically stratified with respect to salinity. The influx of fresh water superimposes upon the regularly oscillating tidal currents a residual or net seaward drift of low salinity water near the surface and a counterdrift of high salinity water near the bottom. The boundary between these layers, the level of no net motion, occurs at about ten feet in depth.

Thus when barnacle larvæ are above ten feet in depth they tend to be transported seawards during a complete tidal cycle, and when below that depth, landwards. The amount of movement, seaward or landward, between successive larval stages will therefore depend on the average depth of the larvæ during that period. Conversely, if the average depths of the larvæ are known, the change in location between successive stages may be used as an indicator of the drift at those depths.

The net direction and velocity of the drift with depth has been calculated from changes in the distribution of successive larval stages of *B. improvisus* initially spawned at the head of the bay (M88, M109C). The vertical and horizontal distribution of each stage was obtained by averaging the results of all plankton samples at stations along the main channel visited during June, July, and August, 1951. The results are shown in Figure 10, which also includes the level of no net motion at 10 feet and the average water transparency at the locations.

Approximately two days after being spawned, nauplius stages I and II were most abundant in surface waters at M109C, 5 miles downriver from M88. A little more than three days later, nauplius III was located at slightly greater depths, mainly at station M110 about 6½ miles farther seaward. At successive intervals of two and one-half days, nauplius IV was most abundant at mid-depths about half-way between M110 and M111 (2 miles still farther seaward) and had dropped below the estimated level of no net motion; nauplius V was perhaps one-half mile seaward of nauplius IV and closer to the bottom, whereas nauplius VI was most abundant close to M110, landward of nauplius V by about 2½ miles. Following a three-day interval, the cyprid population was located back over the beds of original adult spawners at M88, 12 miles above M110, and those not attaching during the first few days were probably carried still farther upriver. During the interval from spawning to 50 per cent attachment (16 days) the seaward and landward component of horizontal movement totalled 28 miles (24·8 nautical miles). The average horizontal velocity of transport during the period was therefore 0·63 n.m.p.h. (3·3 cm./sec.).

On the assumption that the median depth during daylight (Figure 8) is maintained during darkness also, the calculations of the net drift in Figure 10 are given in Table XIV. The median depths during larval development ranged from 6·2 to 15 feet (column 4), and corresponding net current velocities calculated from the 'observed' changes in horizontal location of successive larval stages ranged from 0·09 knot in a seaward direction, through 0 knot at the level of no net motion, to 0·128 knot in a landward direction (column 6). These estimated velocities are within the range of those measured by Pritchard (1952a) at comparable depths in the James estuary when maximum current velocities were about one knot (column 7). Justification for the comparison of Miramichi net velocities (calculated from larval transport) with the measured values in the James estuary is based on the striking degree of similarity of the two

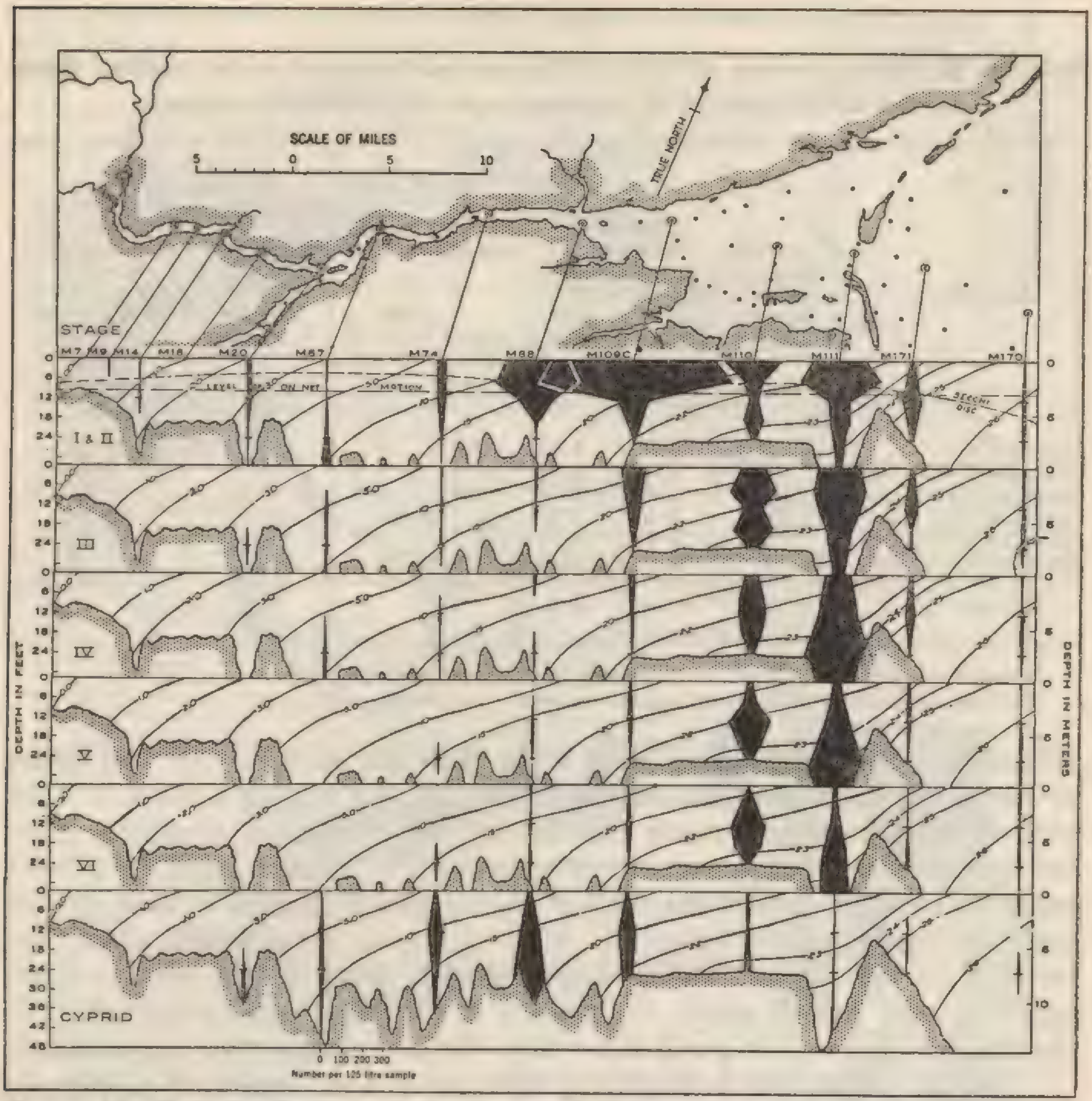

Figure 10. Net distribution of the larvæ of *Balanus improvisus* in the Miramichi estuary during June, July, and August, 1951, in relation to salinity and water currents.

estuaries in discharge, in depth of the channel (25 to 26 feet), in tidal range (4·5 to 5 feet), in the depth of the level of no net motion, and in other respects.

The comparison (columns 6 and 7) shows that the net seaward velocity was greatest near the surface where nauplius I and II were swimming, and least between 11 and 12 feet where nauplius IV and V were taken most abundantly, and that the net landward velocity was greatest near the bottom where nauplius VI and cyprids were most abundant. The level of no net motion, estimated at 10 feet for the Miramichi, appears to be substantially in agreement with that indicated by the net transport of the barnacle larvæ.

The differences in numerical values of the two sets of net velocities may be variously interpreted. The higher net velocities at surface and bottom in the James are probably attributable to the higher maximum

TABLE XIV

Relation of the net current velocity and horizontal transport to the median depth of the larval stage of *B. improvisus* in the Miramichi estuary

(1) Larval stage	(2) Interval between larval stages (days)	(3) Distance transported during interval		(4) (5) Median depth[2] during interval		(6) Calculated[1] net velocity at depths (n.m.p.h.)	(7) Measured net[1] velocity in James estuary at equiv. depths relative to the level of no net motion (n.m.p.h.)
		Miles	Nautical miles	Actual (ft.)	Rel. to level of no net motion		
Nauplius II...........	2	5·0	4·33	6·2	3·8	0·090	0·117
Nauplius II-III.......	3¼	6·5	5·63	6·8	3·2	0·072	0·096
Nauplius III-IV.......	2½	2·0	1·75	9·5	0·5	0·029	0·015
Nauplius IV-V........	2½	0·5	0·43	11·7	−1·7	0·007	−0·052
Nauplius V-VI........	2½	− 2·5	−2·17	13·2	−3·2	−0·036	−0·090
Nauplius VI-cyprid...	3¼	−11·5	−10·5	15·0	−5·0	−0·128	−0·131
Totals............	16	28·0	24·8				

[1] Seaward distance and velocity are positive (+); landward are negative (—).

[2] Distance above the level of no net motion is positive (+); negative below (—).

velocities at those depths (slightly more than one nautical mile per hour) in the James than in the Miramichi (slightly less than 1 n.m.p.h.). The level of no net motion varies throughout the Miramichi estuary. Thus the continued seaward movement of nauplius IV (median depth 11·3 feet) indicates that the level of no net motion was probably greater than 10 feet near the mouth of the estuary. Also, owing to the Coriolis force, the level of no net motion was probably deeper than 10 feet on the south side near the mouth where the middle stages were most abundant, but less than 10 feet on the north side where the late stages were concentrated.

Russell (1935) has exhaustively reviewed the utilization of planktonic "indicator species" in determining the origin of water masses and the circulation in large marine areas. The present results indicate also that observations on the dispersal of barnacle larvæ and similar zooplankton may be used in predicting the circulation of small coastal marine areas such as estuaries in which the hydrography is imperfectly known.

In similar manner, the amount of landward movement of late stage larvæ of *B. crenatus* (Figure 7), swimming as they do well below the level of no net motion (Figure 8), appears to be consistent with the amount of net landward movement of bottom waters along the north side of the estuary and in accord with the Coriolis force.

Dispersal of Other Miramichi Zooplankton

The net distribution of several species of zooplankton was similarly derived from the results of plankton samples along the main channel of the estuary (Figure 11).

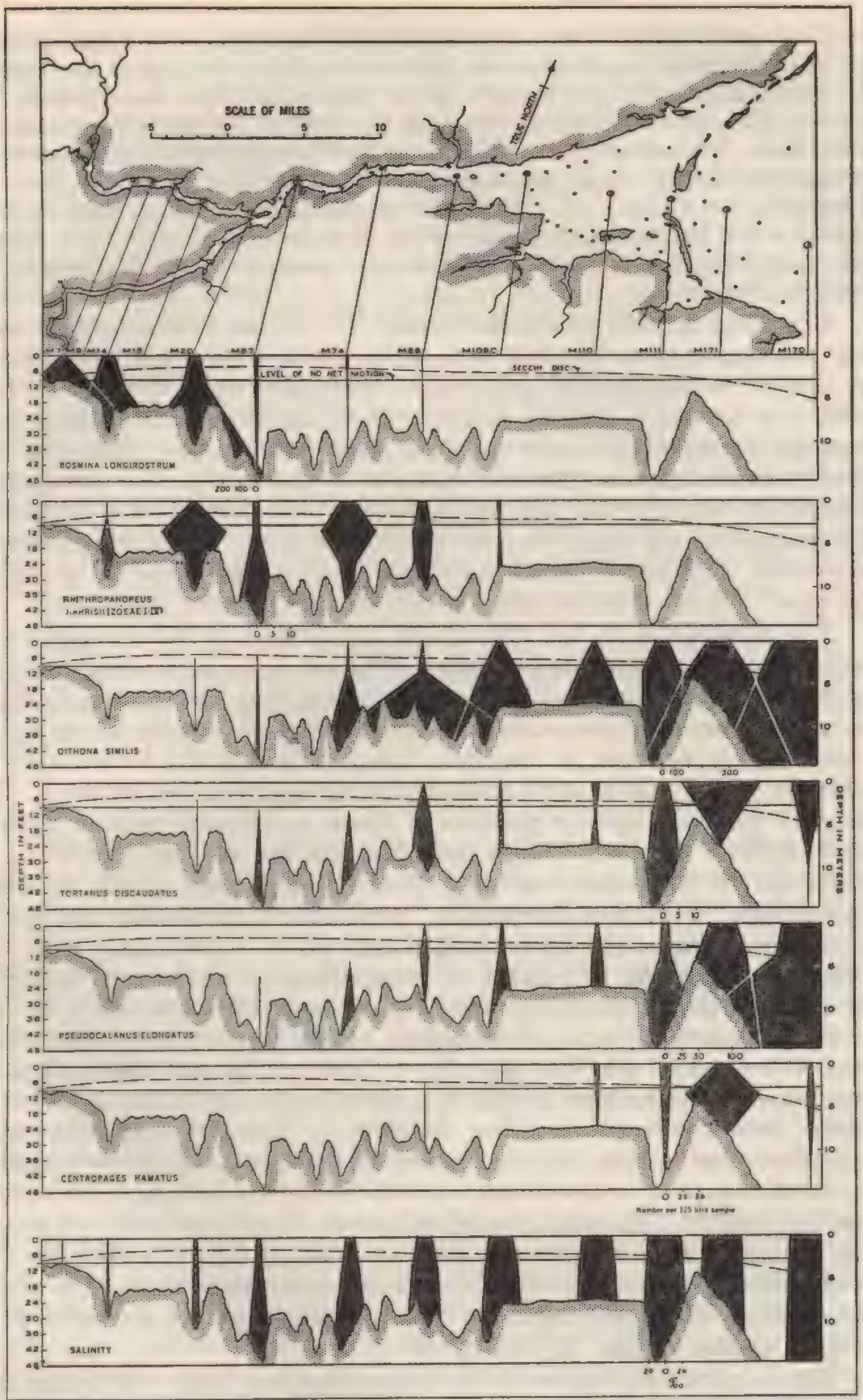

Figure 11. Net distribution of representative planktonic Crustacea in the Miramichi estuary during June, July, and August, 1951, in relation to salinity and water currents.

Bosmina longirostrum, a fresh-water Cladoceran, was found mainly near the bottom in the river above Newcastle, 28·2 miles above the mouth. The few taken from time to time below this point were mainly near the surface. This distribution suggests that the bulk of the upriver population, living near the bottom, are killed or otherwise prevented from moving seaward by the net landward movement of salt water along the bottom. Those near the surface are transported seaward in the net surface outflow of river water but probably perish owing to unfavourable salinities, predation, and other factors which increase in amount or effectiveness in a seaward direction.

The zoeal larvæ (and adults, Table IV) of the brackish-water mud crab *Rhithropanopeus harrisii* were taken mainly from the head of the bay upriver to the limit of salt water. Low salinities (< 20‰) in this region may be a physiological requirement of the species. The larvæ were taken mainly at depths near the level of no net motion. This distributional pattern indicates that the larvæ near the surface are transported seawards, those near the bottom landwards, but that the net horizontal displacement of the population as a whole is zero. Further analysis of the vertical distribution of the individual zoeal stages would be necessary to compare retention in this species with that of *Balanus improvisus.*

The distribution of the adults and late instars of several species of marine copepods may be similar to that of larval stages of *Balanus crenatus* and *B. balanoides,* for which adequate plankton data are lacking. *Oithona similis* and *Pseudocalanus elongatus* were most abundant in deeper strata in the Gulf but occurred in large numbers mainly near the bottom upriver to Middle Island (M74), 20·6 miles above the mouth of the estuary. The fact that the most upriver portions of these populations were comprised almost entirely of adult stages indicates that the upriver population is maintained by landward transport from the Gulf and not by endemic reproduction. *Tortanus discaudatus,* a relatively uncommon species in the estuary, appeared to be most abundant in the Gulf mainly near the surface, although the proportion of copepodites to adults was higher in this species than in the others observed. The adults were taken at and below the level of no net motion upriver almost to Newcastle, 28·2 miles above the mouth. On the other hand, both adults and copepodites of *Centropages hamatus* were located almost entirely outside the estuary and mainly near the surface. The distribution indicates that the same mechanism that results in the landward movement of deep-swimming species of copepods tends to exclude the surface-swimming *Centropages* from the estuary. The dispersal of the larvæ of *Balanus crenatus,* swimming mainly near the bottom, is thus probably much as in *Oithona* and *Pseudocalanus.* The dispersal of the surface-swimming larvæ of *B. balanoides,* whose adults are restricted to the outer fringe of the estuary, is probably similar to that of *Centropages.*

The average distribution of the marine copepods is in contrast to that of salinity (Figure 11), which is determined by tidal mixing and other physical factors. The numbers of salt particles in solution, represented by the figures for the summer average salinity, decrease regularly and gradually from bottom to surface and from the Gulf landward. The decrease in numbers of *Oithona* and *Pseudocalanus* from bottom to surface and landwards was neither regular nor gradual. In *Oithona* there was an abrupt decrease landwards from M88, and in *Pseudocalanus, Tortanus,* and *Centropages* landward from M111. From bottom to surface, particularly inside the estuary towards the innermost limits of each species, the decrease in numbers was abrupt, and out in the Gulf the decrease in number of *Oithona* and *Pseudocalanus* above 12 feet was sharply marked. These comparisons emphasize the importance of vertical swimming behaviour in the dispersal and ultimate distribution of zooplankton.

DISCUSSION AND CONCLUSIONS

The distribution and abundance of barnacles in estuaries are determined by the interplay of ecological factors controlling the survival of the benthic adults and the retention and survival of the planktonic larval stages. The seasonal range of salinity and temperature, the nature of the substratum, and the predation and competition are important factors affecting the survival of adult barnacles. Tidal currents and non-tidal drifts at depths at which the larvæ swim determine the degree of seaward and landward dispersal of the larvæ. Biological factors (e.g. predation) are chiefly important in controlling their survival. The retention of numbers of larvæ sufficient to maintain the adult population is thus a function of dispersal factors and survival factors.

Survival and Distribution of Adult Barnacles

The Miramichi estuary provides a very suitable habitat for the brackish-water barnacle *Balanus improvisus,* but it is less suitable for the marine species *B. balanoides* and *B. crenatus.* Data on annual mortality of these species as adults in the Miramichi were not obtained. Mortality is probably greatest towards the upriver limits of distribution in all species.

The present observations on all three species in the Miramichi estuary substantiate previous theories that lethal low salinities determine the upriver limit of adult barnacles. The most landward populations of *B. improvisus* survived in a range of salinites from 0 to 15‰; those of *B. crenatus* from 6 to 21‰; and those of *B. balanoides* from 12 to 23‰. When these ranges were depressed for prolonged periods by excessive river discharge, the animals were killed.

Other benthic and planktonic organisms associated with the barnacles (Tables IV and IX) probably react similarly to low salinities. The distributions of these forms tend to conform to a subdivision of the estuary into zones of salinity of the Redeke-Valikangas type (p. 6). This system, originally based on studies in the Baltic Sea (of relatively stable salinity) is less easily applied to the Miramichi estuary which has pronounced vertical stratification and wide seasonal fluctuations in salinity. Based on the salinities at mid-depths during average conditions of river flow

(Tables IV and IX, and Figure 5), the estuary is divisible into the following zones of salinity:

Fresh water and oligohaline-brackish (< 3 parts per thousand)	—more than 30 miles above the mouth (above Boishebert I.)
Mesohaline-brackish (3 to 16·5 ‰)....	—16 to 30 miles above the mouth (Cheval Point to Boishebert I.)
Polyhaline-brackish (16·5 to 26 ‰)...	—0 to 16 miles above the mouth (Gulf of St. Lawrence to Cheval Point)
Lower limit of marine water (27 to 28 ‰)	—Gulf of St. Lawrence, off-shore.

The region from Middle Island to Oak Point (11 to 21 miles above the mouth) is most critical to the distribution of coastal marine species. The horizontal gradient of salinity is steepest here (about 1‰ per mile), and very wide changes in salinity take place during tidal ebb and flow (Bousfield, 1955, Figure 7). On the average, however, salt conditions in this region probably approach most closely those of the pleiomesohaline zone (p. 6).

Essentially marine animals, such as *Balanus balanoides* and *B. crenatus, Teredo navalis, Sagitta elegans, Acartia clausi,* and the marine plants *Zostera* and *Fucus* spp., are found mainly in the Gulf and outer estuary. They penetrate landward variable distances into polyhaline waters depending mainly on their vertical distribution. Brackish-water animals, such as *B. improvisus, Rhithropanopeus harrisii, Crassostrea virginica, Eurytemora hirundoides, Acartia tonsa,* and perhaps also certain algæ (*Enteromorpha* sp., and *Coscinodiscus* sp.), are most abundant in polyhaline and mesohaline-brackish zones. They extend seawards into marine water and landwards into fresh water only in much smaller numbers. Fresh-water animals, such as mayfly nymphs, midge and caddisfly larvæ, and *Physa,* and plants (*Scirpus, Potamogeton,* etc.) are limited almost entirely to the fresh-water and oligohaline-brackish zone. *Gammarus fasciatus* is a fresh-water species that is somewhat tolerant of mesohaline-brackish conditions.

The barnacles are widely eurythermal in the vegetative phase of adult life. *Balanus balanoides,* attached to rocks in the tidal zone, is exposed to air temperatures ranging from —30°C. or less in winter to more than 50°C. in summer. *B. improvisus* and *B. crenatus* withstand water temperatures ranging from the freezing point to more than 20°C. The fact that several lots of specimens of *B. improvisus* collected at and just below the low water line in April and early May, 1952, were dead, although the soft parts were still intact, indicates that the species is unable to withstand being frozen into the ice foot that forms along the shore in winter. The fact that *B. balanoides* is more abundant on the north than the south side of the estuary may indirectly be related to water temperatures correspondingly higher on the north than the south side during the winter and early spring. The ice leaves earlier on the north side and exposes the substrata for a longer period, during which the cyprid larvæ may attach. All three species of barnacles are stenothermal during the reproductive phase and spawn only within certain limits of temperature (Bousfield, 1954). Thus the influence of water temperature is felt chiefly on the season of reproduction and on survival of the larvæ.

Also confirmed are the notes by previous investigators (e.g. Moore and Kitching, 1939) that the nature of the substratum determines local areas of abundance and limits of distribution. The scarcity of *B. balanoides* inside the estuary and absence from the sandy barrier islands across the mouth may be attributed to the scarcity or complete absence of rocky outcrops, boulders, and pilings in the tidal zone to which the spat can attach successfully. *B. improvisus* and *B. crenatus,* on the other hand, are able to populate sandy and muddy and otherwise uninhabitable bottoms through the presence of bivalve shells. Although less than 5 per cent of the bottom area is suitable, the density of barnacle populations is high because the cyprids may prolong their planktonic existence, testing the bottom at intervals, until chancing upon favourable substrata.

Severe intraspecific competition for space limits the maximum density of the population in *B. improvisus.* At the same time, however, it probably increases the fecundity of the crowded individuals by assuring successful cross-fertilization and stimulating growth of reproductive tissue. The maximum observed density of new barnacle spat on buoys was approximately one hundred per square inch. Comparable densities were observed on stones, shells, and stakes, in the region of heaviest barnacle populations (Figure 5). After one month's growth on the buoys however, barely thirty tightly packed individuals per square inch had survived.

Interspecific competition for space, and probably also for food, exercises an important limiting effect on the distribution of *B. improvisus* and *B. crenatus* but not of *B. balanoides* in the Miramichi estuary. Organisms that overgrow and smother barnacles are not abundant in the tidal zone of this estuary.

The principal kinds of predators of adult barnacles penetrate into the outer bay from the Gulf and are probably of importance in reducing the abundance of *B. improvisus* in the outer estuary. For instance, *Asterias vulgaris,* a well-known barnacle predator, is barred from inshore waters of the Gulf of St. Lawrence by a combination of high temperatures and low salinities (Smith, 1940). *B. balanoides* has no serious predators in the Miramichi tidal zone, as *Thais lapillus,* the dog whelk, occurs sparsely in the area. The rarity of *B. balanoides* below the low water line in the Miramichi and other areas is probably attributable to predation by starfish (Bousfield, 1954).

The foregoing observations on the ecology of adult barnacles show that suitable conditions for all three species exist in the outer estuary and that differences in distribution and abundance between the species must be the result of factors operating during the planktonic life history.

Survival and Dispersal of Barnacle Larvæ

The number of barnacle larvæ remaining within the estuary (overall survival) bears an inverse relationship to the rate of mortality and seaward dispersal during the period of planktonic development. The present rate of loss of 14·5 per cent per day and overall survival of 10 per cent of the larvæ of *B. improvisus* are of the same order as corresponding values previously obtained in barnacles and other benthic fauna. Pyefinch (1949b) found, through plankton studies in British waters, that the survival of barnacle larvæ, including those of *B. balanoides* and *B. crenatus*, ranged from 1 to 9 per cent. Korringa (1952) estimated that the seaward loss of larvæ of *Ostrea edulis* from the Oosterschelde was 8 per cent per day (4 per cent per tidal cycle). Pyefinch's values are low, because they are based on samples from one depth, one locality, and for a limited period of time. They do not take into account the date of sampling relative to the periods of maximum abundance of the larvæ, nor the differences in both vertical and horizontal distribution of successive larval stages. If Korringa were to add the loss through natural mortality to that of seaward dispersal, the total rate of loss in *O. edulis* would probably be more than 10 per cent per day, and the overall survival about 10 per cent also.

The reliability of the values of survival calculated above depends upon the accuracy with which the duration of the individual larval stages is estimated. The present estimates of larval duration are, in general, similar to those of other regions (Table I). This agreement, coupled with the consistency of results using these figures in studies of larval transport (Table XIV) justifies the assumption that the duration of the individual nauplius stages III to VI of *B. improvisus* is equal. The survival values based on the present estimates of larval duration are therefore believed to be reasonably accurate.

The range of salinities tolerated by the larvæ of *B. improvisus* and *B. crenatus* (Table VIII) does not necessarily establish lethal limits for each species. Larvæ may not reach waters of a given salinity owing to the geographical location of this water with respect to the spawning adults, to the depths at which the larvæ swim, to the net transport of the larvæ by the circulation, and to other factors. The lowest recorded salinities are probably close to the lower lethal limits in each case, however. Upper lethal limits were not measured in the Miramichi, as the highest salinities were less than 28‰. Adults of all three species have been taken in strictly marine habitats (salinites 30 to 35‰) and presumably the larvæ (certainly the cyprid), of each must survive at these high levels.

The wide range of temperature tolerated by larvæ of these species throughout the geographical range, especially in *B. improvisus*, indicates that, as in the American oyster (Loosanoff and Nomejko, 1951), physiological and geographical races are presently included in the delineation of the species. The disappearance of larvæ of *B. balanoides* at the end of May and of *B. crenatus* in June may have resulted from upper lethal water temperatures at those times. The failure of the earliest (mid-May) spawned larvæ of *B. improvisus* is probably attributable to recurring lethal low temperatures (less than 10°C.).

Except in fresh-water parts of the estuary, food of a type suitable for barnacles is undoubtedly abundant and supports a large population of larvæ. On the other hand, there are indications that the phytoplankton may become so numerous as to exclude barnacle larvæ from the water. The diatoms *Chaetoceros* and *Coscinodiscus* occurred in abundance in the outer estuary in June. The bloom of *Coscinodiscus* commenced during the week of June 23 to July 1, and it was during this period that a very great decrease in numbers of most nauplius stages of *B. improvisus* took place (Table XII).

The dispersal of barnacle larvæ is controlled by physical transport and larval swimming. As the population of a given life stage can originate only from that of the previous life stage, the degree of dispersal of barnacle larvæ may be estimated from differences in the steady state pattern of distribution and abundance of successive stages (Figures 6 and 7). These differences in location cannot be explained on the basis of different rates of mortality in different parts of the Miramichi estuary. If larvæ are randomly distributed, natural mortality and seaward loss would result in a continuous decline in the numerical abundance from stage to stage in any part of the estuary. Such is not the case, however. In that part of the estuary above station M109C (head of the bay), nauplius stages II and III are abundant (10 to 200 per sample) and nauplius stages IV and V are almost entirely absent (less than 10 per sample) (Figure 6). Nevertheless, the succeeding larval stages, nauplius VI and the cyprid, occur in larger numbers there (10 to 40 per sample). Also, towards the mouth of the estuary (M111) the numbers of nauplius II and III (61 to 100 per sample) were less than those (79 to 140 per sample) of the succeeding nauplius stages IV and V. Thus changes in distribution of the larval stages are real and are attributable to residual movements of the water, not to differential mortality in different parts of the estuary.

Differences in the vertical distribution of the larval stages may be attributed to specific differences in their vertical swimming behaviour in response to gradients, principally of light, but also of salinity, temperature, food supply, etc. Larval swimming in response to light is different between species, and stages of the same species, and between night and day. Some barnacle larvæ are stimulated by directional light (e.g. Fales, 1928; Visscher, 1928, 1938). In some cases a true kinesis may be involved. If the rate of swimming is proportional to the light intensity, then in strong light the animal would tend to swim faster and remain high up in the water.

The average (median) depth of each larval stage is possibly that at which the intensity of diffuse light, normally the type in surface waters of estuaries, is optimal. That is, animals at higher levels swim down, and animals at lower levels swim up. For example, the early larvæ of *B. improvisus* are found deeper in the Gulf where transparencies are greater, than in the turbid inner estuary (Figure 10). Also an exceptionally large 'break' occurs in the regular decrease in the median depth between nauplius II and III (6·2, 7·8 feet) found in the turbid inner estuary, and that of nauplius IV and V (11·3 and 12·0 feet) found in the more transparent outer bay. Among other zooplankton (Figure 11), adult *Tortanus* and *Centropages* apparently tend to accumulate at high, whereas adult *Oithona* and *Pseudocalanus* are at low, light intensities.

A justifiable criticism of the present theory of plankton retention is that tidal currents and non-tidal drift exist day and night, yet the present data apply only to the daytime vertical distribution and dispersal of the larvæ. The results of studies of diurnal migrations in barnacle larvæ (Pyefinch, 1949b; Visscher and Luce 1928) and in other planktonic marine crustaceans (Esterley, 1920; Nichols, 1933; Johnson, 1938) indicate that the larvæ are probably more uniformly distributed from surface to bottom during darkness than in daylight. Absence of light removes the primary stimulus to directed swimming, and gravitational pull and gradients of salinity may then 'take over' control of vertical distribution.

During June, when *B. improvisus* is spawning, the duration of daylight is twice that of darkness, and the daylight values of vertical distribution are therefore applicable for most of the 24-hour period. If, however, the vertical distribution of all larval stages in darkness is assumed to be nearly uniform from top to bottom, the resultant 24-hour average distribution would be marked by smaller differences in the number of early and late stages between surface and bottom than in those presently derived from daylight plankton samples alone (Figure 8). Thus the actual average depths of nauplius stages II and III would be slightly deeper, and those of nauplius VI and the cyprid slightly higher up than presently indicated. Allowance for night-time vertical distribution may thus partly account for differences in 'calculated' net daytime and 'observed' 24-hour velocities of larval transport (Table XIV). With slight allowances, therefore, the daytime values probably give a reasonably reliable picture of the average 24-hour depth distribution of barnacle larvæ.

With respect to the stimulus for vertical migration provided by gradients of salinity, the present observations are similar to those of Rogers (1940) on barnacle larvæ and Barlow (1953) on copepods. The larval stages of these species were abundant at the surface in the lower estuary where salinities were moderately high at all depths, but occurred mainly near the bottom at upriver localities where surface salinities were consistently low (less than 5‰). Active avoidance of low salinites by such euryhaline species as these thus probably takes place only near the lethal limits of salinity.

The relative importance of the roles played by tidal currents and non-tidal drifts in the dispersal and retention of barnacle larvæ in the Miramichi estuary is suggested by the present investigation. Because of the non-tidal drift at the depths of larval swimming, the seaward loss of barnacle larvæ cannot be predicted accurately from calculations on the loss of neutrally buoyant particles through simple tidal exchanges with the Gulf. This drift tends to retain the larvæ of the estuarine species *B. improvisus* within the estuary; to bring in from the Gulf and concentrate the deep-swimming larvæ of the marine *B. crenatus*; and to exclude from the estuary the surface-swimming larvæ of the marine *B. balanoides*.

The chief influence of tidal currents on the dispersal of barnacle larvæ may be through physical control of vertical distribution. Cyclic changes occur in the vertical distribution of larvæ of *B. improvisus* that are apparently correlated with the velocity of tidal (and wind) currents. Thus nauplius stages II to V are nearest the surface at slack water but deepest at mid-ebb and mid-flood; nauplius VI descends only on the ebb, but the cyprid shows no regular change throughout. All stages, particularly nauplius VI and the cyprid, are closer to the surface at mid-flood than at mid-ebb. At all times, however, earliest stages are nearer to the surface than later stages.

These results agree in part with those of Weiss (1947), who did not find a pattern of vertical distribution in cyprids of *B. improvisus* consistent with stage of tide, but do not agree with those of Pyefinch (1948b), who found no correlation between the abundance (in surface tows) of any larval stage and stage of tide.

The return of late-stage larvæ to the head of the estuary, predicted from the landward direction of drift near the bottom (p. 48), may be accelerated through vertical movements of the larvæ with stage of tide. In estuaries with important residual drifts, mean-ebb velocities are highest near the surface, lowest near the bottom, and mean-flood velocities are highest near the bottom and lowest near the surface (Pritchard, 1952a). Also, velocities at the surface are higher on the ebb than on the flood, but bottom velocities are conversely so. Thus, during ebb tide, vertical turbulence is greatest near the surface but least near the bottom, particularly where the bottom is smooth and regular (i.e. sand and mud), whereas on the flood it is greatest near the bottom and least at the surface. The mechanism postulated by Carriker (1951), by which late-stage oyster larvæ are transported landward, may apply equally well to barnacle cyprids in the Miramichi estuary. The stimulus to rise on the flood need not be salinity, however, but mere mechanical stirring of the water. As strong currents are unfavourable to attachment (Smith, 1946), the cyprid larvæ probably experience greatest difficulty in resting on the bottom during the flood. On the ebb they are not stirred up so violently, thus accounting for more on the bottom at that time. At slack tide, of course, cyprids might be expected to be deepest down and the other larval stages nearest the depth toward which they are stimulated to swim in response to the particular conditions of light and salinity. The probability that the cyprids are more up off the bottom on the flood than on the ebb may explain, at least in part, why the difference between the horizontal location of the cyprid and nauplius VI (11·5 miles) is much greater than that between II and III (6·5 miles), although the interval of transport is similar (3½ days) (Table XIV).

The landward limit of distribution of barnacle larvæ in the Miramichi estuary is determined chiefly by the amount of river discharge during the spawning period. The cyprid larvæ of *B. improvisus* extended more than 40 miles above the mouth during the exceptionally dry summer of 1950, whereas during the rainy summer of 1951 they reached only 30 miles above the mouth. The absence of a 1951-year set of *B. balanoides* at landward localities where adult barnacles had been taken in 1950 suggests that the larvæ of this species were similarly restricted to a point seaward of the 1950 distribution by exceptionally heavy river discharge during April, 1951.

The adults of both *B. crenatus* and *B. balanoides* would probably occur much farther landward in the Miramichi estuary if they were to spawn during the summer rather than in the spring. In the first instance, river discharge is lowest and landward penetration of zooplankton is maximal during July and August, whereas the discharge is highest and penetration minimal during April and May. The cyprids of *B. crenatus*, swimming as they do near the bottom, are capable of being transported landward fully as far as those of *B. improvisus*. The landward limit of the cyprids of *B. crenatus* would probably never reach that of *B. improvisus* because the tolerance of fresh water by the former species is lower. Furthermore, the most landward spat of *B. crenatus* is subjected to prolonged low salinities and to interspecific competition with *B. improvisus, Crassostrea virginica, Modiolus demissus,* and other fouling organisms. Also because of variable river discharge the cyprids of *B. balanoides,* swimming at the surface, would not be transported as far seawards in July and August as they are in April and May. In the second instance, the duration of planktonic existence in both *B. crenatus* and *B. balanoides* would be much shorter in July and August when water temperatures are 18 to 22°C. (provided the larvæ could survive them!) than in April and May when water temperatures are less than 10°C. Thus during the summer, the period in which dispersal of the larvæ can be effected is shorter, the number of cyprids remaining larger, and the population of adults on the bottom greater, than that during spring.

In view of the previous considerations, the presence of *B. balanoides* within the estuary would appear remarkable. The mechanism for the retention of some of the surface-swimming larvæ is not yet clear. Locally spawned larvæ may be carried away from the area, but larvæ from localities farther to the north (e.g. the rocky coast of Gaspé) are probably carried towards it by the counter-clockwise drift in the Gulf. Strong onshore winds and unusually high tides may reverse the net direction of transport for short periods so that more are carried landwards than normally. Since the cyprids of *B. balanoides* are deeper down by night than by day (Pyefinch, 1949b) their net transport at night may be landwards rather than seawards. The abundance of adult barnacles is greater along the north than the south side of the Miramichi estuary because the cyprids are dispersed least from the north shore owing to the influence of the Coriolis force on the pattern of estuarine circulation.

Comparison of Theories of Plankton Retention

The contributions of previous investigators working mainly with other species in other estuaries have stimulated the pursuit of the present problem. The present theory demonstrates the relation between the depths at which the successive larval stages swim and the net transport by the estuarine circulation. It does not, however, duplicate any one previous theory; conversely, no one of the theories developed elsewhere accounts adequately for the observed transport and concentration of barnacle larvæ in the Miramichi estuary.

The main features of the mechanism by which zooplankton are retained in the estuary are (1) a changing vertical distribution of successive planktonic life stages, (2) a residual, or non-tidal drift seawards at the surface and landwards along the bottom, superimposed on tidal oscillation, and (3) a counter-clockwise circulation of the larvæ, completed within the planktonic duration, in the outer estuary.

The present theory differs in all three respects from that of Loosanoff (1949) and Korringa (1952), who found no difference in vertical distribution between early and late stage larvæ of oysters in Milford Harbour and the Oosterchelde, respectively. These authors concluded that the numbers of mature larvæ transported to all parts of the estuary by passive tidal conveyance alone were sufficient to account for the observed density of attachment on available substrata. It also goes beyond the theory of

Barlow (1953) in points (1) and (3). The observed steady state distribution of *Acartia tonsa* in Great Pond was explained on the basis of the natural rate of increase of the population, and on the "refuge" from seaward dispersal offered (presumably to all life stages) by the residual landward drift of salt water in the deeper layer. Although his data indicate that differences in the vertical distribution between the life stages of this copepod exist, such were not related to the horizontal differences in the concentration of nauplii, copepodites, and adults throughout the pond (p. 63).

The counter-clockwise transport of barnacle larvæ around the Miramichi estuary is superficially similar to that of calanoid copepods around a much larger semi-enclosed basin, the Gulf of Maine (cf. Redfield, 1941). The circulation and maintenance of the copepod population, however, result from mass transport by drift currents presumably similar in direction and velocity throughout the depth range of the life stages, whereas that of larval barnacles result from differences in the direction and velocity of water movement at the different depths of each life stage.

The present theory also shows the influence of more factors, chiefly in points (2) and (3), than do the theories of Nelson and Perkins (1931), Roughley (1933), and Carriker (1951), who found differences in vertical distribution between early and late stage larvæ of oysters, and between stages of tide, but did not clearly differentiate the roles of tidal currents and non-tidal drift in the landward movement of the late-stage larvæ.

It is most closely approached on points (1) and (2) by Huntsman (1945, 1951) and Rogers (1940), both of whom worked with barnacles, other sessile and planktonic invertebrates, and certain estuarine fishes. From observations that adult *Balanus improvisus* and *Rhithropanopeus harrisii* were found in the inner but not in the outer part of the Miramichi estuary, Huntsman concluded that the planktonic larvæ of these animals must be near the bottom most of the time lest they be carried seawards by the surface drift. The present results show, however, that (in the case of *B. improvisus*) the adults are abundant in both inner and outer estuary, and that only the late stage larvæ are near the bottom most of the time, the early stages being near the surface and moving seaward. Rogers (1940) attributed the concentration of larvæ (presumably of *B. improvisus*) near the head of tide in the St. John estuary to landward drift in the deeper layers. The larval stages composing the population were not distinguished, however, and thus differences in vertical distribution between stages were not detected. His theory of retention by means of diurnal migrations, originally derived from smelt larvæ (p. 13) does not appear to hold in the case of *B. improvisus* and *B. crenatus* in the Miramichi estuary but may apply in reverse (p. 60) to that of *B. balanoides* on the outer coast.

Dispersal and Retention in Other Zooplankton

The distribution of other zooplankton in the Miramichi estuary (Figure 11) indicates that the mechanism of dispersal and retention applying to the larvæ of barnacles applies equally well to other species of zooplankton in the area. Fresh-water forms are apparently transported downriver and killed, presumably by lethal high salinities. Marine plankton is carried in along the bottom, and estuarine populations are maintained by continuous recruitment from the Gulf.

The retention and concentration of estuarine plankton such as the larvæ of *Rhithropanopeus* may be similar to that of larvæ of *B. improvisus*. The adults and larvæ of this crab occur only in the river. All larval stages tend to remain at or just below the lower boundary of the seaward drift (level of no net motion) and thus would not be carried downstream to any great extent. As the adult crabs spawn late in July and August, when river discharge is lowest, the larvæ are probably transported a maximum distance upriver. The retention of large populations of *Acartia tonsa* and *Eurytemora hirundoides* (Table IX) in the river and head of the bay may also result from a landward transport of breeding adults to replace the seaward loss of surface-swimming nauplii.

The control of larval dispersal in other sessile marine bottom invertebrates of the Miramichi estuary (Table IV) may be similar to that in barnacle larvæ (see below). For instance, the oyster *Crassostrea virginica* has very similar ecological requirements to the barnacle *B. improvisus* in the Miramichi estuary. Their estuarine distribution, spawning periods, and length of planktonic existence are closely comparable, and the behaviour of adults and larvæ in response to gradients of temperature, salinity, and to substratum, competition, and other factors are basically similar.

The early stage larvæ of both *Crassostrea* and *B. improvisus* are found near the surface, late stages near the bottom, and are transported in similar degree by the net drift at those depths. Oysters of marketable value are taken in Baie du Vin, inside Vin Island, and at Egg Island, and a large population of low grade 'fresh-water' oysters are found above Sheldrake Island almost to Newcastle (Medcof, 1943). The researches of Butler (1949) indicate that oysters living for most of their life in low salinities at upriver localities do not spawn. However, the upriver population is very probably maintained by a landward movement of larvæ from the bay similar to that in barnacles.

During July and August of normal years, the numbers of late stage oyster larvæ carried by tidal ebb and flow to all parts of the lower estuary are probably sufficient to produce a good set, in spite of seaward transport at the surface and upriver loss of the bulk of the late stages at the bottom. In cold years (as in 1950), however, the reduction in spawning may drop below the amount necessary to offset depletion by water transport and to produce a good spatfall. The landward drift may explain why early stage larvæ are often taken at one station for a few days, but subsequent stages become much less numerous and finally disappear completely.

Application of the Present Theory to Other Estuaries

The present theory of plankton retention stresses the role of changes in the average vertical distribution of successive larval stages of an estuarine barnacle in relation to the amount and direction of transport by residual drift at those depths. The distribution of oyster larvæ at Milford Harbour, as determined by Prytherch (1928), illustrates how the present theory may be applied to the retention of benthic marine organism in other estuaries having a similar type of circulation. The presence of only very early and very late larval stages of *Crassostrea virginica* in the Harbour is strikingly paralleled by the presence of comparable stages of *B. improvisus* above Sheldrake Island in the Miramichi estuary. Carriker (1951) had postulated, on the basis of Prytherch's belief, that spawning took place only at high water, that oyster larvæ were carried seaward on the ebb, but that the late stages "worked back again" by swimming up off the bottom mainly on the flood. However, it is more probable that early stage oyster larvæ, regardless of the stage of tide at spawning, were carried seaward by the surface drift in Milford Harbour and that deep-swimming late-stage larvæ were transported back to the original spawning beds by residual landward drift of salt water along the bottom.

A second example is provided by the distribution of the holoplanktonic copepod *Acartia tonsa* in Great Pond, which Barlow (1953) has explained in terms of replacement rate (p. 61). Barlow's data show, however, that the nauplii were concentrated near the head and nearer the surface than the bottom, that copepodites were farther seaward and somewhat deeper down, and that the adults were deepest of all, but in largest numbers towards the head. Because of the drift circulation in this small estuary, is it not probable that the surface-swimming nauplii are carried towards the mouth, sinking as they go, but, on metamorphosing to copepodites, drop into landward moving water and finally reach the head again as spawning adults? The large number of spawning adults in the headwaters would thus account for the high rate of replacement of nauplii found by Barlow in that region.

The present theory does not apply to larval movements in estuaries such as the Oosterschelde (Korringa, 1952) with little residual drift and small tidal exchange with the sea, nor such as Barnstable Harbour with small residual flow but large tidal exchange (Ketchum, 1952), nor the Margaree (Rogers, 1940) where there is a considerable drift and a large tidal exchange also. In the first instance a residual transporting mechanism is not present. In the latter two cases, endemic populations of benthic marine animals such as *Mya arenaria* and *B. improvisus* do not exist; the life cycles cannot be completed within those estuaries owing to the great excess of seaward loss of larvæ over reproductive increment.

SUMMARY

1. The purpose of the present study was to determine the occurrence of the acorn barnacles *Balanus improvisus, B. crenatus,* and *B. balanoides* in the Miramichi estuary, New Brunswick, and to investigate how these animals may be maintained near the head of the estuary despite the severity of ecological conditions and the net discharge of water to the sea.

2. The Miramichi is a coastal plain estuary averaging 13 feet in depth at low water, and its 50-mile length is divisible into an inner narrow 'river' part and an outer 'bay' part that broadens to its mouth at the Gulf of St. Lawrence. The circulation is marked by (*a*) a water exchange with the gulf of 15 per cent per tidal cycle, (*b*) a large and seasonably variable influx of fresh water from the Miramichi watershed, and (*c*) a residual

or non-tidal seaward drift of water within 10 feet of the surface, strongest on the south side, owing to the Coriolis force, and a residual landward drift below that depth, strongest on the north side of the estuary.

3. Dredging and inshore collecting for adults, and special seasonal sampling of newly attached barnacle larvæ (spat) showed that (*a*) *Balanus improvisus* is most abundant in the shallows of the bay and lower river but scarce in the gulf and in the river within 20 miles of the head of tide, (*b*) *B. crenatus* occurs abundantly in the gulf but diminishes landward to the head of the bay, and that (*c*) *B. balanoides* occurs in the tidal zone of the gulf coast and outer part of the bay mainly along the north side. *Balanus improvisus* and *B. balanoides* were not taken as far up the estuary in 1951 as in 1950 owing to the high mortality of the most landward adult barnacles and the restricted landward penetration of the planktonic larvæ during exceptionally heavy freshets in 1951.

4. With respect to the environmental control of adult survival (*a*) low salinity is probably the chief factor that sets the upriver limit in all three species, (*b*) winter freezing prevents *B. improvisus* from permanently colonizing the tidal zone, (*c*) predation may be an important factor restricting *B. improvisus* to the estuary and *B. balanoides* to the tidal zone, and (*d*) intra- and inter-specific competition for space limits the population density in *B. improvisus* and *B. crenatus* respectively.

5. The distribution and abundance of the six nauplius stages and the cyprid of *B. improvisus* and *B. crenatus* have been deduced from more than five hundred plankton pump samples, taken at weekly intervals during the summer of 1951 in longitudinal, lateral, and vertical axes in the Miramichi estuary. In *B. improvisus* the early nauplii were located mainly near the head of the bay, later nauplii near the mouth, and the cyprid again near the head; in *B. crenatus* the early nauplii were mainly near the mouth, later nauplii farther landward, and the cyprid farthest landward. In *B. balanoides* all larval stages probably occur only in the Gulf and near the mouth of the estuary.

6. The average depth at which barnacle larvæ swim, chiefly in response to light intensity, changes with the life stage. In *B. improvisus* early stages are found at 6·2 feet, middle stages at about 12 feet, and the cyprid at 15·4 feet; in *B. crenatus* the first five stages occur at about 12 feet and the cyprid at 17·4 feet. Both early and late stages of *B. balanoides* are probably within 6 feet of the surface.

7. The vertical position of the larvæ of *B. improvisus* changes with the stage of tide and with the velocity of vertical currents. The nauplii are nearest the surface at high and low water, and deepest at mid-ebb and mid-flood; the cyprids are farthest above the bottom on the flood.

8. The average planktonic life of *B. improvisus* during June and July totals eighteen days; four days for the first two nauplius stages combined; two and one-half days for subsequent nauplius stages, and four days for the cyprid. The rate of loss owing to mortality and seaward transport of the larvæ is 14·5 per cent per day. Of the larvæ initially spawned 10 per cent remain inside the estuary eighteen days later (at the time of attachment), and the numbers are sufficient to maintain the observed adult population in the estuary.

9. If the larvæ of *B. improvisus* displayed a uniform vertical distribution, tidal exchanges with Gulf waters during eighteen days would deplete the population below the level necessary to maintain the adult population. The special mechanism by which barnacles are maintained in the Miramichi estuary is shown by the present investigation to be the relation between the depths at which the successive larval stages drift and the estuarine circulation. The residual drift transports early stage larvæ of *B. improvisus,* found near the surface, to the mouth of the estuary, whereas it carries the deep-swimming late stages back up the estuary to (and beyond) the original spawning sites. The effect is augmented by the cyprids being higher in the water during the flood than the ebb tide. By the same mechanism the later larval stages of *B. crenatus* are carried in from the Gulf to the limit of their low salinity tolerance, but those of *B. balanoides,* swimming near the surface, tend to be carried out of the estuary especially during periods of river flood. The seaward transport of the three species is strongest on the south side, and the landward movement strongest on the north side of the estuary.

10. No one of the concepts of estuarine circulation developed elsewhere accounts adequately for the situation in the Miramichi. The present investigation demonstrates a three-dimensional movement of water that is caused by the combined action of river discharge and tidal currents in the presence of a density (salinity and temperature) gradient under the influence of the Coriolis force. The vertical distribution of the larvæ changes with the life stage and with the phase of tide in such a way that the larvæ are carried by the vertically and horizontally varying residual drift to suitable areas in the estuary where adult populations can be maintained.

11. The distribution of other sessile benthic animals (i.e. adults of *Crassostrea virginica*) and of certain types of zooplankton (i.e. the larvæ of *Rhithropanopeus harrisii,* and adults of *Acartia tonsa*) in the Miramichi estuary indicate that the mechanism of dispersal and retention of many species is similar to that for barnacles. The same mechanism is undoubtedly in operation in other coastal plain estuaries that similarly display pronounced vertical differences in direction and velocity of residual drifts.

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